Landscape Use By Gulls (*Larus* spp.)

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"Statistics are like bikinis. What they reveal is suggestive, but what they conceal is vital."

Prof. Aaron Levenstein (1930-1986)

Abstract

In contrast to the negative impacts of landscape change on many aspects of biodiversity, scavenging bird species, like gulls (*Larus* spp.), have reacted positively and expanded their ranges. This in turn has brought a number of problems, including; damage to town centres, an increased risk of disease transmission to humans, domestic animals and livestock, an increased risk of collision with aircraft and a threat to vulnerable seabird populations. A great deal of money has been invested in measures to mitigate these problems. However, these have often been hampered by a failure to understand the ecology of the system concerned.

This study employs a variety of statistical techniques to investigate factors related to the spatial and temporal distribution of gulls, the possible problems they may cause and the efficacy of measures to reduce the impact of these problems. Using structural equation modelling (SEM) it was possible to show that in contrast to other groups, like corvids which use landfill sites close to their roosts throughout the year, gulls rely most heavily on landfill sites as a source of food during the winter. However, analysis of the spatial distribution of winter gull roosts using negative binomial generalised linear models (GLMs) showed that only roosts of the black-headed gull (*Larus ridibundas*) were positively influenced by proximity to landfill sites. In contrast to the winter, when roosts were widely distributed, during the summer roosts had a coastal distribution.

The problems posed by gulls to air safety and human health were investigated by analysing the spatial patterns of accidents and the incidence of salmonella carriage by

wild birds. In the first, bivariate k-means clustering revealed that strikes on Royal Air Force (RAF) aircraft by gulls were clustered within the 6 km surrounding major (>1000 individuals) gull roosts and landfill sites. These results were used to identify additional areas capable of supporting large numbers of gulls, and hence likely to represent a threat to aircraft in the future. I used survival analysis to investigate temporal and spatial patterns in wild bird salmonella. Passerines were more likely to be infected with salmonella than non-passerines and further analysis was indicative of gulls having a higher rate of salmonella infection than other non-passerines. Salmonella prevalence in wild birds was greatest during the winter and spring, and in areas with large populations of cattle. Having investigated the factors determining where gulls were and the risks they posed to aircraft safety and human health, I analyse the efficacy of a range of management techniques to control problem gull populations, using linear mixed effects models (LMEs). This revealed that techniques with occasional lethal events were the most effective. By using a range of statistical techniques, it was possible to disentangle a series of complex and often interacting relationships between gulls, the landscape and humans.

Acknowledgements

There are a large number of people whose help has made this thesis possible. My supervisor, Prof. Steve Rushton, has provided me with a unique insight into the academic mindset, and has ensured that my research has been both challenging and enjoyable. Together with Dr. Roy Sanderson, he has ensured that I leave Newcastle with at least a grasp of how to use linux, grass and R, not to mention statistics. Much of my work would have taken far longer were it not for the help of Dr. Mark Shirley, showing me little tricks and shortcuts for sorting data in Excel and Access.

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Chapter 1: Introduction

As a result of human activity, the landscape of the United Kingdom has been dramatically altered in recent years with changes to agricultural practices and loss of green space (Burnside *et al.* 2003; Pauleit *et al.* 2005; Perry & Nawaz 2008). These changes have had a dramatic impact on the nation's avifauna. Agricultural intensification and changes in arable practices have led to dramatic falls in the populations of many farmland birds (Krebs *et al.* 1999; Donald *et al.* 2001; Newton 2004). Increases in sheep numbers have contributed to the decline of upland species, like the red grouse (*Lagopus lagopus scoticus*) (Fuller & Gough 1999; Thirgood *et al.* 2000). Even species otherwise well adapted to urbanised areas have declined in response to increasing housing density (Tratalos *et al.* 2007).

In contrast, these changes have enabled many other species to thrive, with some even associated with high human population densities (Jokimaki & Suhonen 1998). Town centres can provide a steady and predictable food supply, structures for new nesting habitats and reduced levels of predation and persecution (Vuorisalo *et al.* 2003; Marzluff & Neatherlin 2006). In particular, gull (*Larus* spp.) populations have increased rapidly in response to the abundant food supplied by areas like landfill sites (Horton *et al.* 1983), whilst also taking advantage of the nesting opportunities offered by roof tops (Monaghan & Coulson 1977; Raven & Noble 1997). I will investigate what aspects of these changes have enabled gulls to expand their ranges and what impacts this has had.

Gull Populations in the United Kingdom

There are six species of gull which regularly occur and breed in the United Kingdom, the common gull, *Larus canus* (Plate 1.1), the black-headed gull (*Larus*

Plate 1.1 The Common Gull, *Larus canus* (Photo used with permission, R. Robinson)

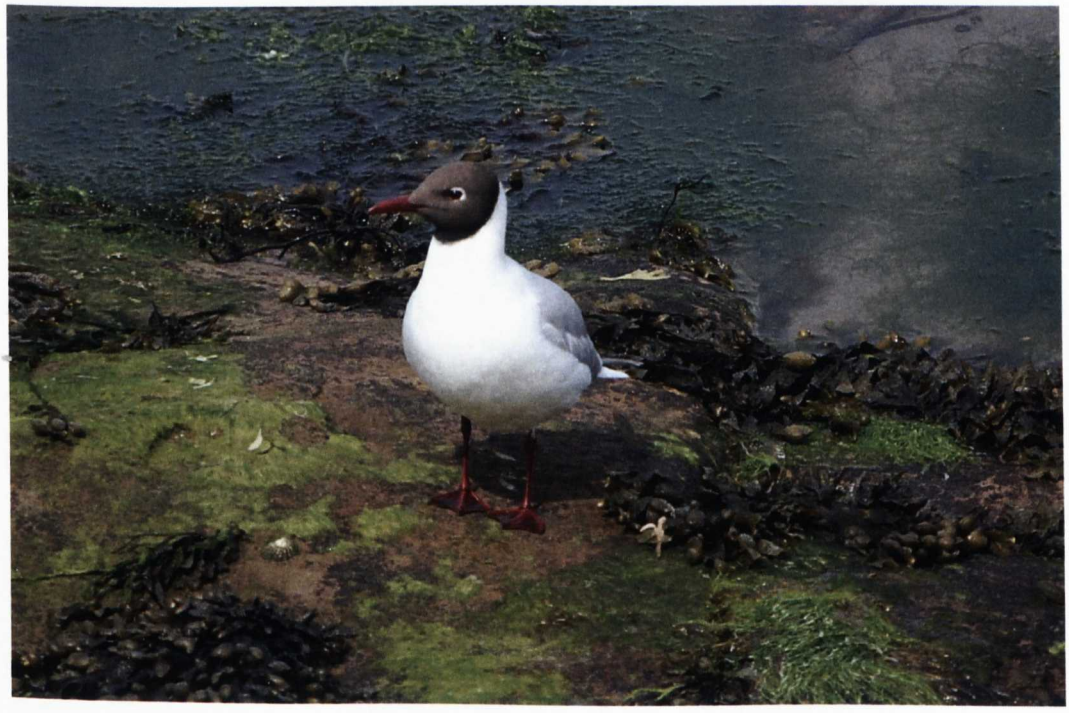


Plate 1.2 The Black-headed Gull, *Larus ridibundas*

Plate 1.3 The Herring Gull, *Larus argentatus*

Plate 1.4 The Lesser Black-backed Gull, *Larus fuscus*

Plate 1.5 The Great Black-backed Gull, *Larus marinus*

ridibundas)(Plate 1.2.), the herring gull (*Larus argentatus*)(Plate 1.3.), the lesser black-backed gull (*Larus fuscus*)(Plate 1.4), the great black-backed gull (*Larus marinus*)(Plate 1.5.) and the black-legged kittiwake, *Rissa tridactyla*. The United Kingdom contains a number of sites, like Walney Island in Cumbria, which host internationally important breeding populations, defined as 1% or more of the biogeographic population, of each of these species (Stroud *et al.* 2001; Mitchell *et al.* 2004; Table 1.1). Breeding populations of the common, herring and great black-backed gulls remain relatively stable, although they have experienced moderate increases. In contrast, the lesser black-backed gull population has undergone dramatic increases and the black-headed gull has experienced an equally dramatic population decrease (Raven & Noble 2001).

	Breeding Population	% Biogeographic Breeding Population	% Change in Breeding Population 1994-2000	Winter Population
Black-headed Gull *Larus ridibundas*	138 014	3	-20.3	1 697 797
Common Gull *Larus canus*	48 720	15	8.3	430 927
Lesser Black-backed Gull *Larus fuscus*	112 074	71	34	60 830
Great Black-backed Gull *Larus marinus*	17 160	5	1.5	43 156
Herring Gull *Larus argentatus*	139 309	6	5.8	378 748
Kittiwake *Rissa tridactyla*	379 892	12	*	**

Table 1.1 Population trends and status of UK gull populations (Raven & Noble 2001; Stroud *et al.* 2001; Mitchell *et al.* 2004; Baker *et al.* 2006), * no estimates available for population trends in the kittiwake. ** the UK breeding population of the kittiwake winters in the Atlantic Ocean.

ridibundas)(Plate 1.2.), the herring gull (*Larus argentatus*)(Plate 1.3.), the lesser black-backed gull (*Larus fuscus*), the great black-backed gull (*Larus marinus*)(Plate 1.4.) and the black-legged kittiwake, *Rissa tridactyla*.The United Kingdom contains a number of sites, like Walney Island in Cumbria, which host internationally important breeding populations, defined as 1% or more of the biogeographic population, of each of these species (Stroud *et al.* 2001; Mitchell *et al.* 2004; Table 1.1). Breeding populations of the common, herring and great black-backed gulls remain relatively stable, although they have experienced moderate increases. In contrast, the lesser black-backed gull population has undergone dramatic increases and the black-headed gull has experienced an equally dramatic population decrease (Raven & Noble 2001).

The smaller species, the black-headed and common gulls, begin to breed after 2-3 years, whilst the larger species begin breeding after 4-5 years. They typically lay clutches of 3 eggs between May and June every year, although clutches of up to 7 have been reported for the herring gull (Summarised Cramp *et al.* 1983). The age at first breeding is related to hatching date, with those hatching earliest breeding at the youngest age (Prevot-Juillard *et al.* 2001). The proportion of chicks fledging then improves year on year as birds become more experienced (Rattiste 2004). However, every year there is a significant proportion of adults, usually those which are small or "poorer" quality, which do not breed (Calladine & Harris 1997; O'Connell *et al.* 1997).

During the breeding season gulls attend roosts colonially with the kittiwake, herring, lesser and great black backed gulls favouring coastal areas and black-headed and common gulls favouring upland areas (Cramp *et al.* 1983; Mitchell *et al.* 2004).

Coloniality brings with it a number of costs including; the increased risk of transmission of parasites and disease, increased risk of cuckoldry, intraspecific competition for food and mates, cannibalism and infanticide (Brown & Brown 1986; Brown et al. 1990; Danchin & Wagner 1997). These costs are balanced by a number of benefits including; reduced predation risk as a result of the dilution effect and an increase in the number of vigilant individuals to watch for possible predators, enhanced foraging efficiency, as colonies act as "information centres" for food finding, the increased availability of extra-pair copulations and increased chick immunity as a result of higher yolk antibody concentrations (Brown 1967; Brown 1988; Morton *et al.* 1990; Barta & Szep 1995; Richner & Heeb 1995; Brown & Lang 1996; Terhune & Brillant 1996; Malickiene & Budrys 2002; Muller *et al.* 2004). Nests tend to be in vegetated areas which allows for the protection of chicks and eggs from adverse weather conditions and concealment from predators (Montevecchi 1978; Calladine 1997; Kim & Monaghan 2005). However, in recent years there has been a dramatic shift of breeding individuals away from their natural habitats and into industrial or urban areas where they have access to a plentiful supply of food and protection from predators (Raven & Coulson 1997). This has had no discernable effect on breeding success (Soldatini *et al.* 2008).

At the end of the breeding season, the gull population of the United Kingdom undergoes massive changes (Table 1.1). Lesser black-backed gulls disperse towards continental Europe, Iberia and North Africa (Galavan *et al.* 2003) and kittiwakes disperse westwards into the Atlantic (Cramp *et al.* 1983). However, the populations of gulls, notably the lesser black-backed gull, overwintering in the UK have undergone massive increases since 1953 (Bowes *et al.* 1984; Burton *et al.* 2002). The UK

populations of black-headed, herring and great black-backed gulls are supplemented with immigrants from Scandinavia and continental Europe (Cramp *et al.* 1983; Coulson *et al.* 1984a,b; MacKinnon & Coulson 1987; ; Baker *et al.* 2006). Populations of these species start to build up from the end of the breeding season at the end of July until November, with a peak arrival occurring during September. The populations then start to disperse again during December and by the end of February-beginning of March, wintering birds have returned to their breeding grounds.

Interactions Between Man and Gulls

The increasing use of anthropogenic habitats by gulls has brought them into contact with man on a daily basis. Gulls are frequently observed roosting on reservoirs, feeding on landfill sites, around fisheries discards, sewage outflows and in town centres, as well as loafing on agricultural land and playing fields (Vernon 1972; Cramp *et al.* 1983; Horton *et al.* 1983; Sibly & McCleery 1983; Greig *et al.* 1986; Belant 1997; Belant *et al.* 1998; Ferns & Mudge 2000; Arcos *et al.* 2001; Burger 2001; Garthe & Scherpe 2003; Yorio & Caille 2004; Schwemmer & Garthe 2005; Plate 5.). Whilst some of these interactions may be benign, many others bring gulls into conflict with people.

Plate 5. There are a number of ways gulls come into contact with people including, feeding on fisheries discards and landfill sites or loafing on playing fields and agricultural land

Gulls have been found to harbour a range of pathogens infectious to both humans and livestock including; *Salmonella* (Kapperud & Rosef 1983; Ferns & Mudge 2000; Wahlstrom *et al.* 2003; Nesse *et al.* 2005; Palmgren *et al.* 2006; Cizek *et al.* 2007), C*ampylobacter* (Kapperud & Rosef 1983; Broman *et al.* 2002), *Clostridium botulinum* (Ortiz & Smith 1994; Neimanis *et al.* 2007), *Escherishia coli* 0157 (Wallace *et al.* 1997; Fogarty *et al.* 2003; Nelson *et al.* 2008), infectious bursal disease virus (Hollmen *et al.* 2000) and highly pathogenic avian influenza H5N1 (Ellis *et al.* 2004). Estimates of the prevalence of these diseases in wild gulls range from 0.9% (Wallace *et al.* 1997) of the population for E-coli up to 36.2% for *Campylobacter* (Broman *et al.* 2002). Strains of both *Salmonella* and *Campylobacter* have been isolated which are common to both humans and gulls (Broman *et al.* 2002; Nesse *et al.* 2005; Palmgren *et al.* 2006).

The use of areas like landfill sites and sewage outflows may be linked to *Salmonella* carriage by gulls (Fenlon 1983; Kapperud & Rosef 1983).However, they appear to be clinically unaffected by *Salmonella* (Palmgren *et al.* 2006) and their ability to travel large distances, utilising a wide range of anthropogenic habitats raises the possibility of transmitting this zoonotic infection to people. This is of particular concern given the isolation of antibiotic resistant strains of *Salmonella* from gulls (Cizek *et al.* 2007).

Large aggregations of gulls can pose a risk to air safety. The first human fatality resulting from a collision between birds and aircraft involved a gull in 1912 (Thorpe 2003). Between 1990 and 2005 in the United States, gulls were responsible for 6 201 collisions with aircraft at a cost of US$24 153 973 and 41 360 hours of aircraft downtime (Cleary *et al.* 2006). The majority of strikes occur around airports (Milsom & Horton 1995) and are therefore relatively easy to prevent using deterrence techniques, to ensure large numbers of birds are not able to gather in the area (i.e. Dolbeer *et al.* 1993; Belant 1997; Gilsdorf *et al.* 2002). As the distribution of strikes away from airports is harder to predict, they are also harder to prevent. However, they are also more likely to cause damage than those occurring around airports (Dekker *et al.* 2006). Gulls are of particular concern given their large body size and tendency to flock (Allan *et al.* 1999; Dolbeer *et al.* 2000; Carter 2001).

A great deal of money has been invested in investigating possible solutions to these problems. Bird avoidance models (BAMs) are used to prevent en-route collisions between aircraft and gulls (i.e. Lovell & Dolbeer *et al.* 1999; Alexander *et al.* 2002). These use the distribution of birds to map areas of potential risk to aircraft however,

they often operate at too coarse a scale to be of practical use (Dekker & van Gasteren 2005). The traditional approach to keeping pest gulls away from sensitive areas, like airports or landfill sites, is to harass them with one or more of a suite of deterrence techniques like falconry (Baxter & Allan 2006), shooting (Dolbeer *et al.* 1993; Baxter & Allan 2008), dogs (Carter 2000) or distress calls (Baxter & Robinson 2007; Soldatini *et al.* 2008). However, these are often subject to the effects of habituation. Recently alterations to the habitat surrounding areas like landfills or airports, and changes in human behaviour have been advocated as ways to keep gulls from problem areas (Brough & Bridgman 1980; Gabrey & Dolbeer 1996; Belant 1997; Ferns & Mudge 2000; Burger 2001; Martinez-Abrain *et al.* 2004; Blackwell *et al.* 2008).

A more drastic solution is to try and limit the size of roosts using strategies like culling and making eggs unviable (i.e. Christens & Blokpoel 1991; Bosch *et al.* 2000; Guillemette & Brousseau 2001; Finney *et al.* 2003; Martinez-Abrain *et al.* 2004). However, these can often have unexpected results. Making eggs unviable can increase colony reproductive success by decreasing the levels of intra-specific competition (Martinez-Abrain *et al.* 2004). Culls have to be repeated year on year as the effects of dispersal and meta-population dynamics mean that any individuals removed from a population are replaced by gulls from elsewhere (Bosch *et al.* 2000). All of these techniques could be better implemented with the incorporation of an improved understanding of the ecology of the system in the decision making process.

Thesis Aims

The aims of this thesis are to investigate how an understanding of the temporal and spatial variation of both gulls, and hazards associated with gulls can be used to inform management decisions. This will be achieved using a variety of modelling techniques to interrogate a number of datasets. The first two chapters deal with the spatial and temporal distribution of gulls and consider how their reliance on human altered landscapes varies throughout the year in response to life history characteristics, like breeding and migration. Following this, two specific problems associated with gulls will be considered. Firstly, I will investigate how the distribution of roost sites influences the distribution of gull collisions with Royal Air Force (RAF) aircraft in England and Wales, and how this information can be used to mitigate this problem. Secondly, I will investigate how *Salmonella* prevalence in wild birds varies throughout the year and in response to land use. I will then assess the efficacy of a range of widely used deterrence techniques at keeping gulls away from landfill sites.

Sutherland *et al.* (2006) identified 100 ecological questions of direct relevance to policy makers. Of these, three are of relevance to this thesis:

1. *What are the direct (catch) and indirect (food supplementation by discards, prey depletion) impacts of commercial fishing on cetaceans and seabirds?*

Gulls are often observed feeding on fisheries discards, particularly during the summer (Furness *et al.* 1992; Garthe & Scherp 2003). As part of chapter 3, I will investigate how the size and distribution of fishing ports influences the size and distribution of gull roosts during the summer and winter.

2. *How can we understand better the epidemiology of existing and emergent diseases within wildlife reservoirs to better protect humans and livestock?*

Gulls host a number of pathogens which are potentially hazardous to both humans and livestock. Using the example of *Salmonella*, I will show how disease prevalence in wild birds can vary in space and time, as well as being influenced by human land use.

3. *With what precision can we predict the ecological impact of different policy options and the ecological effects of management action?*

Attempts to control problem populations often have unexpected consequences (Martinez-Abrain *et al.* 2004). Throughout this thesis I will argue that a better understanding of the ecology of the system involved makes it possible to better predict the results of any management action and therefore develop more effective management strategies.

By failing to take ecology into account when developing strategies to control pest species, many management strategies have failed. Factors such as density dependence, meta-population dynamics, carrying capacity and spatial autocorrelation all influence where a species is and more importantly why it is there. Consequently, to manage these species it is vital to take these factors into account.

Many previous studies have failed to do so, and consequently have not achieved what they set out to. A recent example of this that has received a great deal of press and public attention is the role of badgers (*Meles meles*) in the transmission of bovine tuberculosis (BvTB). Between 1975 and 1997 over 20 000 badgers were culled in the United Kingdom to control BvTB (Donnelly *et al.* 2003). However, results indicate that this cull not only failed to control BvTB, but may have actually caused it to

increase (Donnelly *et al* 2003, 2006; Woodroffe *et al.* 2006). This is because the culls caused the dispersal of badgers over a wider area, meaning that infected individuals came into contact with a larger number of cattle and other uninfected badgers.

Predatory Gulls often pose a problem to breeding waders and seabirds. In order to improve breeding success in these species, Gulls from surrounding colonies are often culled (Harris & Wanless 1997; Bosch *et al.* 2000; Guillemette & Brousseau 2001). However, these culls often have limited effect as they need to be continued over multiple years, do not take sufficient account of the effects of immigration from neighbouring colonies and it is often difficult to cull sufficient numbers to have a noticeable impact.

By using a range of statistical techniques to interpret long term ecological datasets, I aim to ask three key questions:

- How do gulls use the landscape?
- What problems does this cause?
- What measures can be taken to prevent these problems occurring?

By understanding how and why gulls use the landscape in the way they do, it will be possible to get a better understanding of how the resultant problems occur and what can be done to counteract them. Whilst doing this I will aim to ensure that any assumptions made are valid both in terms of the ecology of the species concerned and also the problem being investigated. I will use analytical techniques that can account for many of the problems associated with ecological datasets, like repeated measures, pseudo-replication and spatial and temporal autocorrelation. Having done this I will

aim to show how consideration of the ecology of the system concerned is vital for its effective management.

Chapter 2: The use of structural equation models (SEM) to develop management strategies: the problem of scavenging birds on landfill sites

Abstract

A wide range of scavenging birds, notably gulls and corvids, use landfill sites opportunistically as a source of food. This has a number of undesirable side-effects including the possible spread of disease, a threat to aviation safety, damage to nearby urban areas and general disruption to site operations. Previous studies have identified spatial and temporal differences as well as human activity as potential sources of variation in bird abundance at landfill sites. Control of these species is often unsuccessful. A key reason for this is that organisms within the system are often subject to a series of interacting, multi-factorial processes. We used structural equation modelling (SEM), a powerful technique which uses multiple equations to model multivariate relationships, to investigate and compare the importance of factors affecting the abundance of 9 avian species - herring gull, *Larus argentatus*, black-headed gull, *Larus ridibundas*, lesser black-backed gull, *Larus fuscus*, great black-backed gull, *Larus fuscus*, starling, *Sturnus vulgaris*, rook, *Corvus frugilegus*, jackdaw, *Corvus monedula* and carrion crow, *Corvus corone* – on 6 UK landfill sites. We identified 2 major sources of variation. Gull species tended to be most strongly affected by temporal variation, while, in contrast, corvids tended to be most strongly affected by spatial variation. These results are discussed in the context of the ecology of the species concerned, and their likely interactions with existing control strategies. SEM enabled us to account for these responses and better understand the underlying patterns within the data, potentially enabling the development of more focussed, cost-effective species management. Whilst we have considered a system where the species concerned are pests, this could equally be applied to the management of a system where the species involved are of conservation concern.

Introduction

Humans have dramatically altered the landscape of the United Kingdom in recent years, with serious consequences for the nation's avifauna. Processes such as urbanisation (i.e. van den Berg *et al.* 2001; Lilley & Clarke 2003; Devictor *et al.* 2007) and agricultural intensification (Pain *et al.* 1997) have resulted in the loss and fragmentation of the habitats of a wide range of species. However, despite these losses, some species have been able to adapt to the opportunities offered by these changes and thrive. Some, such as gulls, are able to take advantage of artificial nesting sites offered by roof tops (Monaghan & Coulson 1977; Raven & Coulson 1997), whilst others such as geese take advantage of agricultural land for foraging (Newton & Campbell 1973). Knowledge of how and why species adapt to such changes has important management implications both in terms of the conservation of rare species and the control of pest species.

The United Kingdom generates 400 million tonnes of waste per annum, equivalent to 1 600 tonnes per kilometre squared. However, this waste is transferred, concentrated and stored in a small number (1 222) of landfill sites (HM revenue and customs 2006). This concentration of resources at a relatively small number of foci has led to the exploitation of landfill sites for foraging by a diverse range of scavenging species, notably gulls (*Larus* spp.) and corvids (*Corvus* spp.). In effect, landfill sites can be considered as "bird tables" for the landscape, replenished on a daily basis, often with a large volume of food, and attracting large numbers of birds. Unfortunately, these birds bring with them a number of problems including interference with the day to day operation of waste disposal (Baxter 2005), an increased risk of collision with aircraft (CAA 2007; Burger 2001), damage to nearby town centres (Vermeer *et al.* 1988) and the possible spread of

human pathogens such as *Salmonella* spp (Monaghan *et al.* 1985; Ferns & Mudge 2000) and *Escherichia coli* 0157 (Wallace *et al.* 1997).

As a result of these problems, large sums of money are invested in deterring species from areas such as landfill sites and airports, where large concentrations of birds cause serious problems (Allan 2002). However attempts to control are often hampered as the extent to which birds forage on landfill sites can vary spatially (Duhem *et al.* 2003), seasonally (Karlsson 2003), hourly (Coulson *et al.* 1987) and by species (Wells 1994). In order to develop effective and efficient management plans to minimise the impacts of scavenging birds on landfill sites, it is necessary to understand the relative importance of each of these sources of variation. However, this is a multi-factorial problem which is likely to involve a series of interacting processes. Consequently, a technique that will allow the development and evaluation of models of complex relationships is required to evaluate the impacts of environment, land management and the likely effects of population control.

Structural equation modelling (SEM) is a powerful statistical tool that has only recently been applied to ecological questions. In contrast with traditional, univariate approaches, which are limited in the number of processes they can examine, and therefore can often be misleading when investigating complex systems, SEM uses multiple equations in order to model multivariate relationships (Grace 2006). When using SEM, a hypothesised model based on an *a priori* knowledge of the relationships in the system concerned is developed. This model is then challenged with the data and appropriately simplified, until a parsimonious model remains. We aim to show how SEM can be applied to investigate the use of landfill sites by scavenging birds, which require management and discuss how our findings can be used to inform decisions about any necessary intervention.

Methodology

Data Collection

Hourly counts of feeding and loafing behaviour for the 9 bird species most commonly observed on landfill sites(black-headed gull, great black-backed gull, lesser black-backed gull, herring gull, common gull, Carrion crow, jackdaw, rook and starling) were collected from 6 UK landfill sites over the period 19 July 2000 to 1 April 2002. The sites were characterised by being on the edge of towns and surrounded by large areas of farm and grassland. Erin landfill site (SK447718) was visited on 350 days during the study period, Heathfield (SX865765) 201 days, Peckfield (SE445335) 148 days, Pilsworth (SD819088) 136 days, Risely (SJ667935) 91 days and Whitehead (SJ701989) 213 days. The duration of visit and number of counts depended on seasonal patterns in photoperiod, and birds were counted either between dawn and mid-day or mid-day and dusk. Waste delivery activity and bird control procedures were recorded whenever these took place during the sampling period. Weather related variables, temperature (°C), precipitation, cloud cover (octas) and wind force (Beaufort scale) were recorded at the same time as birds were counted.

Transformation and calculation of variables

As the bird abundance data were counts, they were log transformed prior to analysis. Behavioural patterns of diurnal and migratory birds are likely to be cyclic, accordingly all of the temporal variables were sine transformed prior to analysis so that cyclic activity patterns could be analysed. Finally, photoperiod for each of the days within the study period was calculated using the methodology of Sharpley & Williams (1990).

Structural Equation Models

Structural equation modelling (SEM) was used to investigate the pattern of relationships amongst the weather, control and tipping variables and their likely impacts on bird

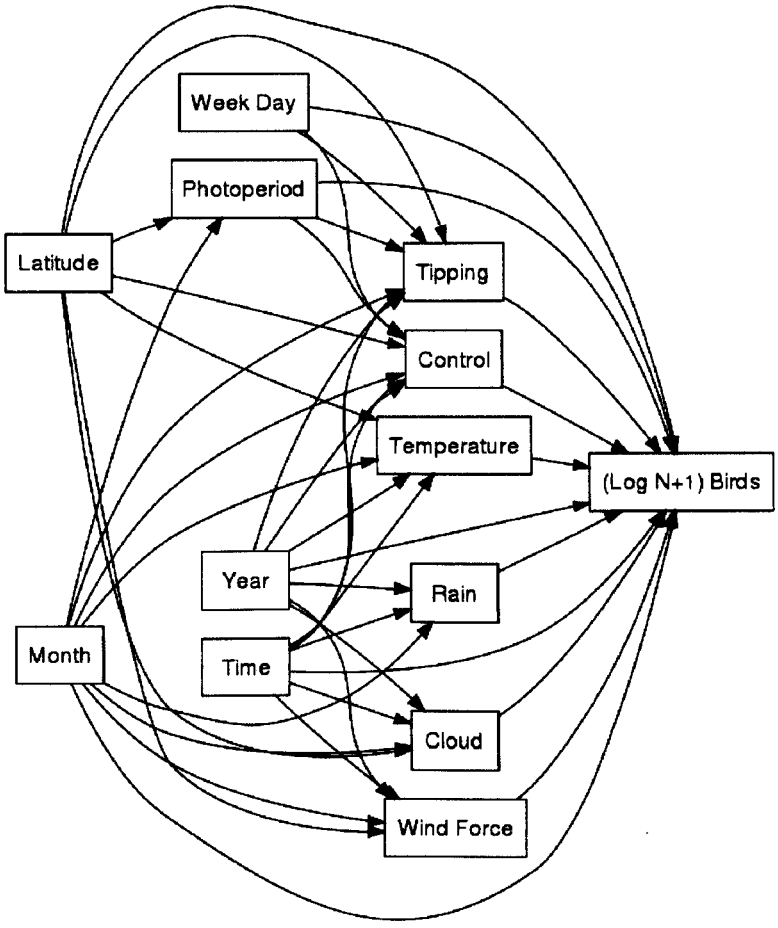


Figure 2. 1. Initial hypothesised model predicting bird abundance on landfill sites

counts. A hypothetical model of the causal relationships amongst the variables in a system, based on *a priori* hypotheses of the likely role of each variable in the modelled system, was developed (figure 2. 1.)

It was assumed that seasonal patterns related to bird demography, for example migration, weather and human activity would be the most important factors determining bird abundance. In effect bird abundance on landfill sites as a response would be dependent on;

i) The seasonal cycle as an exogenous variable, with migratory species, like the Herring Gull being more abundant in the winter relative to resident species like the Carrion Crow.

ii) Diurnal pattern as an exogenous variable, with birds showing a pattern typified by arriving from their overnight roosts at day break and peaking by mid-day.

iii) Landfill site location as an exogenous variable, with the pattern of species abundances varying regionally.

iv) Photoperiod, with fewer hours of day light restricting each species potential foraging time and encouraging them to use landfills, and, in addition, the spatial variation in photoperiod causing regional differences in landfill use.

v) Weather, with poor conditions likely to make widespread foraging more energetically costly, with poorer returns, and therefore encouraging birds to make use of reliable food sources, such as landfill sites. Low ambient temperatures also require more energy to be diverted to thermoregulation, also necessitating access to a reliable food source (Norstrom *et al.* 1986).

vi) Tipping activity, where birds would either be encouraged by the arrival of "fresh" waste, or disturbed by the increased human activity

vii) Bird control having a negative impact on the numbers of each species present

viii) A temporal pattern in the delivery of new food resources, and control measures, with both control and tipping cyclic processes and less in evidence at the weekend.

In contrast to the temporal and spatial variables, the effects of weather and human activity are not independent of seasonal and diurnal patterns. They were therefore modelled as endogenous variables, in that they were not only predictors of bird abundance, but were themselves dependent on the spatial and temporal variables.

The hypothetical model for each species was tested using the available data. The models were then compared with simpler models from which non- and weakly significant pathways had been removed. Due to the high sample size, Chi^2 tests (where a significant Chi^2 indicates that the model is not supported by the data) were not necessarily a reliable assessment of the model (Grace 2006). Consequently, goodness of fit was also assessed by comparing the Comparative Fit Index (CFI), Root Mean Square of Approximation (RMSEA), Goodness of Fit Index (GFI) and Bayesian Information Criterion (BIC) of each model. All models were fitted using the SEM extension in R 2.2.0 (Fox 2006; R Development Core Team 2006).

Results

None of the initial models for any species were adequate representations of the data. For all species the removal of weakly and non-significant variables to create more parsimonious models substantially improved the measures of fit. The most parsimonious SEM's are presented here (figures 2.2 2-2.10).The signs of the coefficients for weather variables indicate that it was warmer and less windy during the summer (figs. 2.2-2.10), and that it tended to be wetter, windier and cloudier during the beginning and end of the day with peaks in temperature in the mid-morning (figs. 2.2-2.10). They also indicated site specific differences in temperature and wind force (figs. 2.2-2.10). There was some

indication that temperature may be important for some species, with most being associated with lower temperatures. However, in general, the coefficients indicated that the birds showed a weak response to changes in weather (table 2. 1.).

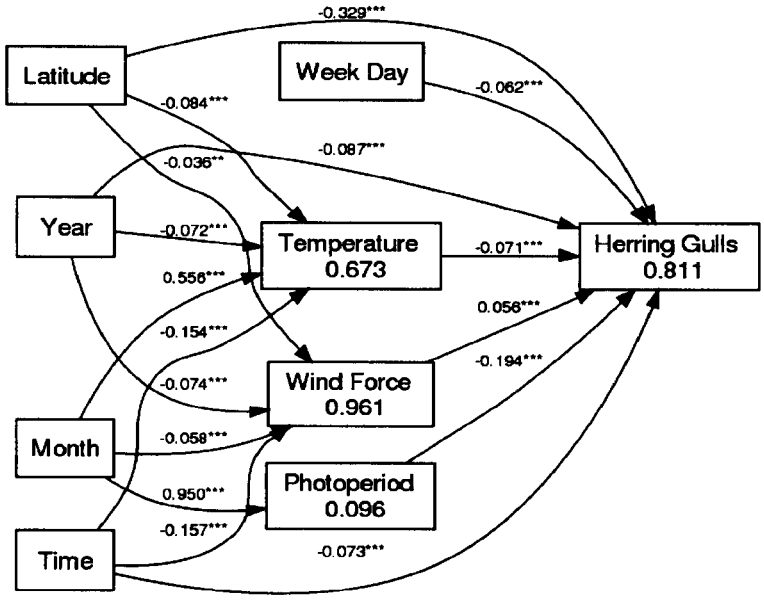


Figure 2. 2 The most parsimonious SEM for herring gull abundance on landfill sites, χ^2 1826.6, d.f 20, P<0.01, RMSEA 0.10, CFI 0.93, GFI 0.95, BIC 1645.3, also reported are the U path coefficients (proportion of variation unexplained) for each endogenous variable(in boxes) and size, direction and p-value (* P<0.05, ** P<0.01, ***P<0.001) for each relationship (alongside pathways)

	Herring Gull		Black Headed Gull		Lesser Black Backed Gull		Great Black Backed Gull		Common Gull		Carrion Crow		Jackdaw		Rook		Starling	
	I.E	T.E	I.E	T.E	I.E	T.E	I.E	T.E	I.E	T.E	I.E	T.E	I.E	T.E	I.E	T.E	I.E	T.E
Latitude	-0.004	-0.333	-0.006	0.092	-0.030	0.088	-0.006	-0.210	0.000	0.075	0.029	-0.253	-0.008	0.027	0.025	-0.378	-0.007	0.212
Month	-0.226	-0.226	-0.156	-0.321	-0.075	0.127	-0.190	-0.350	-0.055	-0.358	-0.078	0.055	-0.208	0.037	0.069	0.036	0.331	-0.110
Week Day	-	-0.062	0.022	0.022	0.021	0.021	-0.008	-0.008	0.018	0.018	0.015	-0.056	-0.050	-0.050	0.003	-0.038	-	-0.065
Day Length	-	-0.194	0.016	-0.188	-0.031	-0.151	-	-0.165	0.021	0.021	n/s	n/s	0.050	-0.214	n/s	n/s	-	0.319
Year	0.004	-0.083	-0.011	-0.208	-0.052	-0.285	0.030	-0.055	0.011	0.011	-0.042	-0.098	0.009	-0.047	-0.033	-0.073	-0.011	-0.187
Time	0.001	-0.072	-0.004	-0.040	-0.011	-0.117	0.012	-0.035	0.011	-0.033	0.009	0.009	-0.021	-0.059	0.008	0.008	-0.023	-0.023
Tipping	n/s	n/s	-	0.075	-	0.107	n/s	n/s	-	0.074	n/s	n/s	-	-0.162	n/s	n/s	n/s	n/s
Control	n/s	n/s	n/s	n/s	-	-0.122	-	-0.088	-	-0.045	-	0.171	-	-0.039	-	0.126	n/s	n/s
Temp.	-	-0.071	-	0.050	-	0.115	-	-0.080	-	-0.072	-	-0.100	n/s	n/s	-	-0.095	-	0.058
Precip.	n/s	n/s	n/s	n/s	-	0.064	n/s	n/s	n/s	n/s	n/s	n/s	n/s	n/s	n/s	n/s	-	0.062
Cloud Cover	n/s	n/s	-	0.023	n/s	n/s	n/s	n/s	n/s	n/s	-	-0.064	n/s	n/s	-	-0.072	n/s	n/s
Wind Force	-	0.056	n/s	n/s	n/s	n/s	n/s	n/s	n/s	n/s	-	0.062	-	0.083	-	0.070	-	0.072

Table 2. 1 Indirect (I.E.) and total effects (T.E.) of variables affecting the presence of scavenging birds on landfill sites, direct effects are shown on figures 2..2-10. n/s indicates variable insignificant and not included in final model, - indicates variable had no indirect effect. Indirect effects are calculated by summing the products of each pathway, for example latitude affects herring gulls through two indirect pathways (via temperature and wind force). The direct effect of latitude on temperature is -0.084 and on wind force is -0.036. The direct effect of temperature on herring gulls is -0.071 and the direct effect of wind force on herring gulls is 0.056, so the indirect effect of latitude on herring gulls is (-0.084 x -0.071) + (-0.036 x 0.056). The total effect of a variable is the sum of its direct and indirect effects.

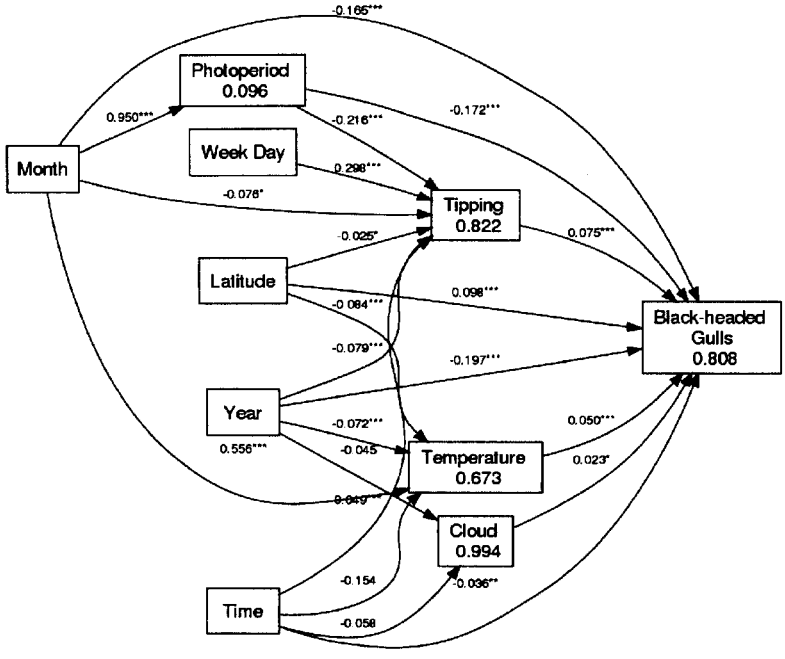


Figure 2. 3 The most parsimonious SEM for black-headed gull abundance on landfill sites, χ^2 1788.9, d.f 25, P<0.01, RMSEA 0.09, CFI 0.93, GFI 0.96, BIC 1562.3, also reported are the U path coefficients (proportion of variation unexplained) for each endogenous variable (in boxes) and size, direction and p-value (* P<0.05, ** P<0.01, ***P<0.001) for each relationship (alongside each pathway).

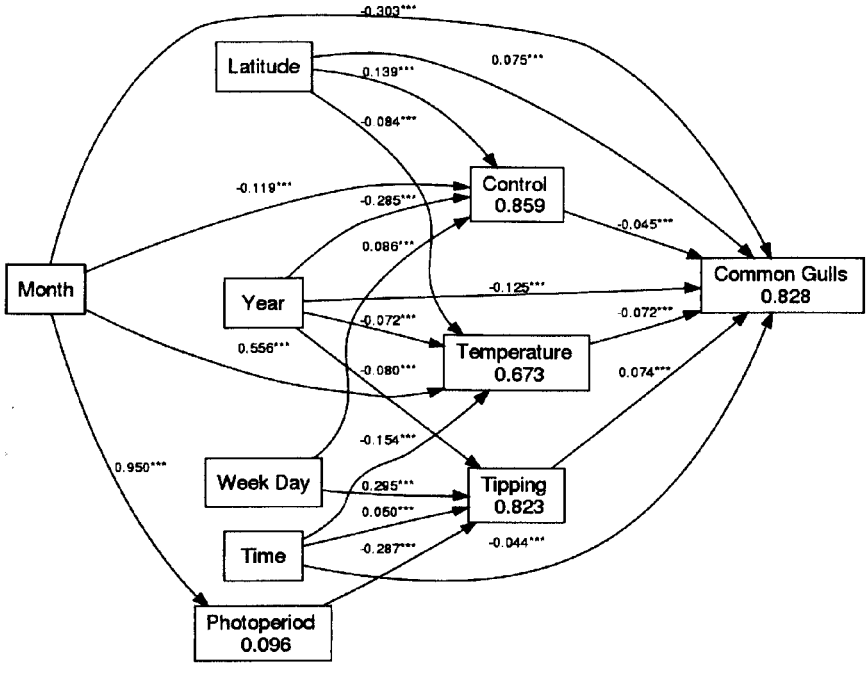


Figure 2. 4 The most parsimonious SEM for common gull abundance on landfill sites, χ^2 1980.4, d.f 25, P<0.01, RMSEA 0.09, CFI 0.93, GFI 0.96, BIC 1753.8, also reported are the U path coefficients (proportion of variation unexplained) for each endogenous variable (in boxes) and size, direction and p-value (* P<0.05, ** P<0.01, ***P<0.001) for each relationship (alongside each pathway).

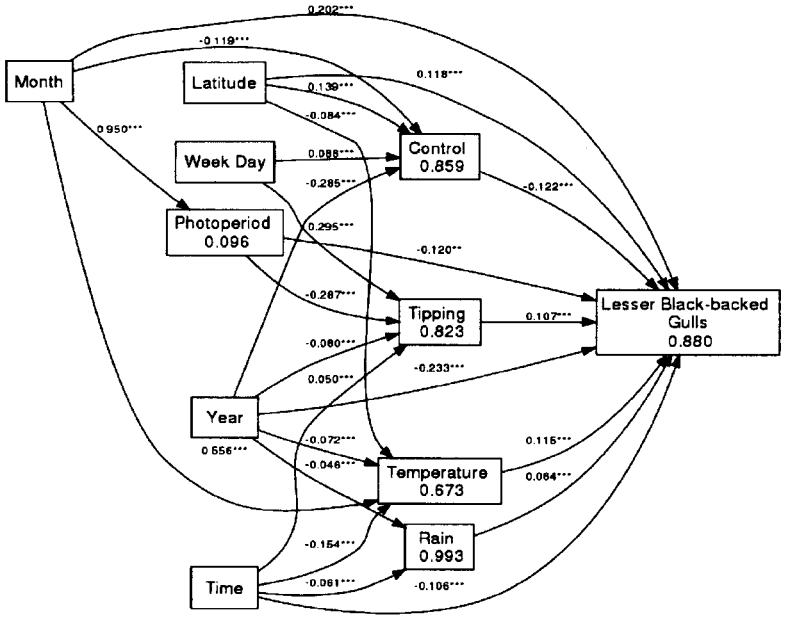


Figure 2. 5 The most parsimonious SEM for lesser black-backed gull abundance on landfill sites, χ^2 2095.0, d.f 31, P<0.01, RMSEA 0.09, CFI 0.93, GFI 0.96, BIC 1814.1, also reported are the U path coefficients (proportion of variation unexplained) for each endogenous variable (in boxes) and size, direction and p-value (* P<0.05, ** P<0.01, ***P<0.001) for each relationship (alongside each pathway)

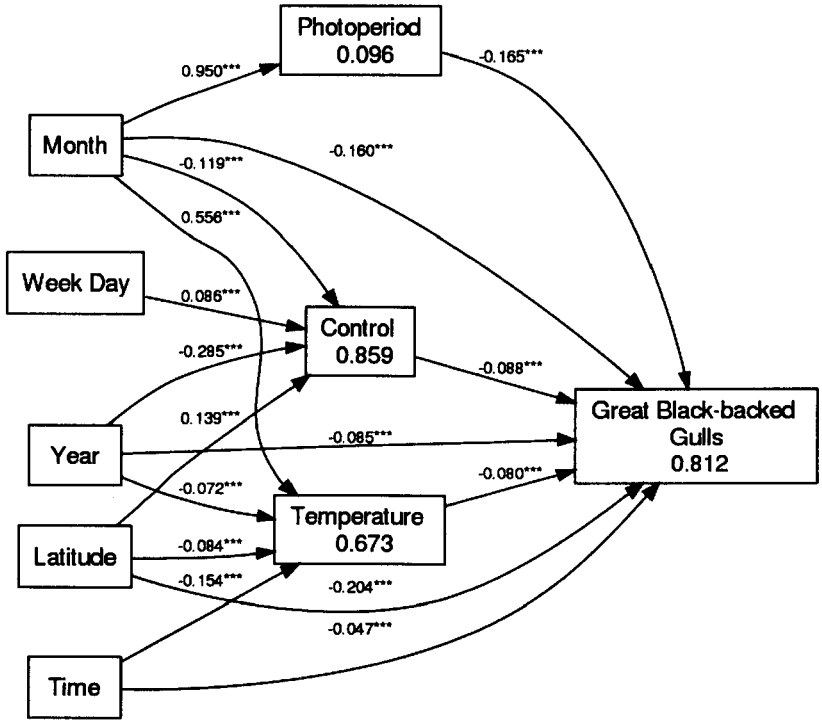


Figure 2. 6 The most parsimonious SEM for great black-backed gull abundance on landfill sites, χ^2 1730.2, d.f 20, P<0.01, RMSEA 0.10, CFI 0.94, GFI 0.96, BIC 1548.9, also reported are the U path coefficients (proportion of variation unexplained) for each endogenous (in boxes) variable and size, direction and p-value (* P<0.05, ** P<0.01, ***P<0.001) for each relationship (alongside each pathway)

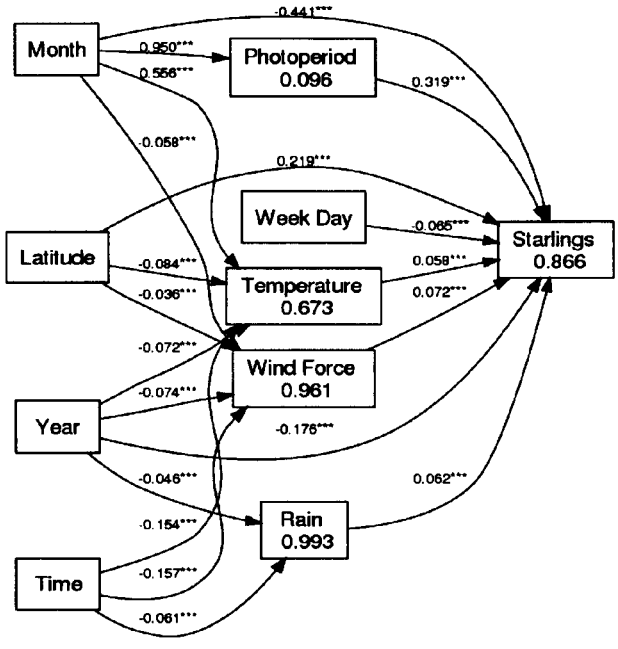


Figure 2. 7 The most parsimonious SEM for herring gull abundance on landfill sites, χ^2 2105.4, d.f 26, P<0.01, RMSEA 0.09, CFI 0.93, GFI 0.96, BIC 1779.7, also reported are the U path coefficients (proportion of variation unexplained) for each endogenous variable (in boxes) and size, direction and p-value (* P<0.05, ** P<0.01, ***P<0.001) for each relationship (alongside each pathway)

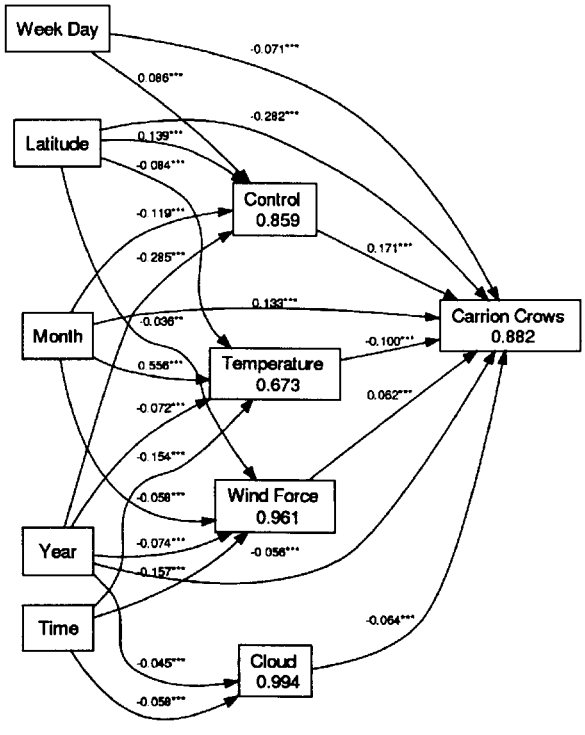


Figure 2. 8 The most parsimonious SEM for carrion crow abundance on landfill sites, χ^2 710.5, d.f 23, P<0.01, RMSEA 0.06, CFI 0.90, GFI 0.98, BIC 502.0, also reported are the U path coefficients (proportion of variation unexplained) for each endogenous variable (in boxes) and size, direction and p-value (* P<0.05, ** P<0.01, ***P<0.001) for each relationship (alongside each pathway)

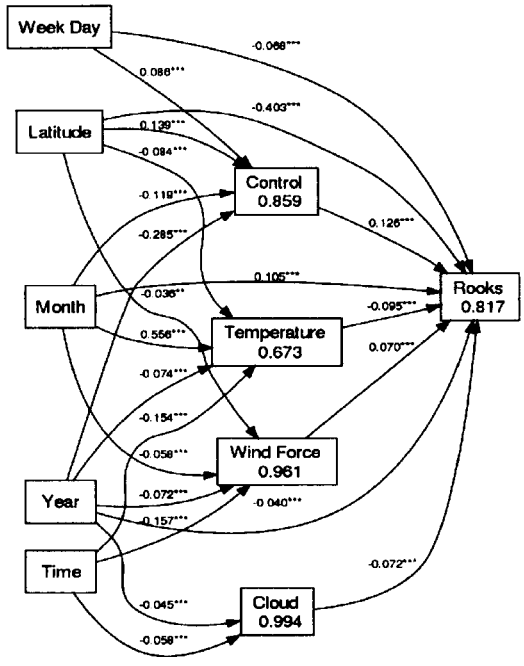


Figure 2. 9 The most parsimonious SEM for rook abundance on landfill sites, χ^2 718.4, d.f 23, P<0.01, RMSEA 0.06, CFI 0.91, GFI 0.98, BIC 509.9, also reported are the U path coefficients (proportion of variation unexplained) for each endogenous variable (in boxes) and size, direction and p-value (* P<0.05, ** P<0.01, ***P<0.001) for each relationship (alongside each pathway)

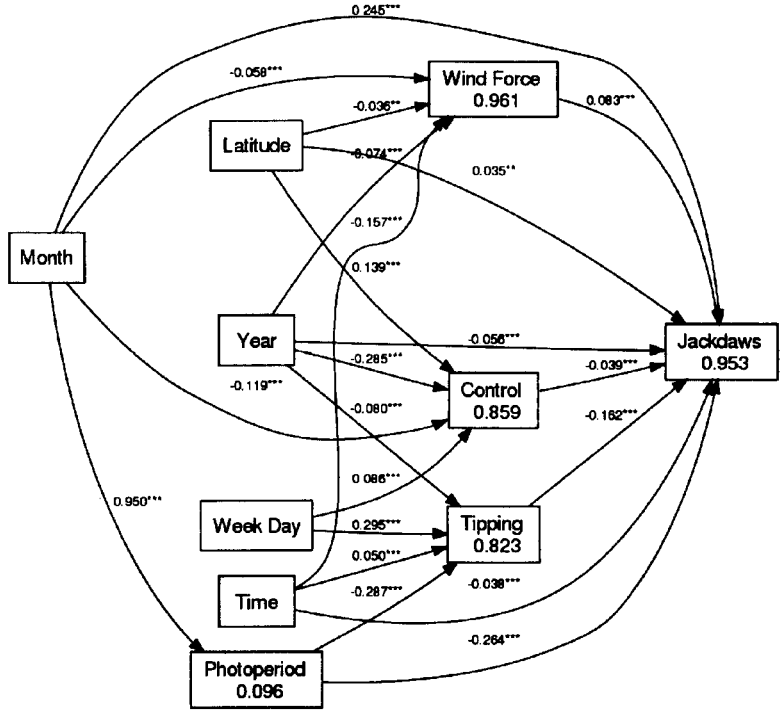


Figure 2. 10 The most parsimonious SEM for jackdaw abundance on landfill sites, χ^2 659.8, d.f 24, P<0.01, RMSEA 0.06, CFI 0.97, GFI 0.98, BIC 442.3, also reported are the U path coefficients (proportion of variation unexplained) for each endogenous variable (in boxes) and size, direction and p-value (* P<0.05, ** P<0.01, ***P<0.001) for each relationship (alongside each pathway).

The variables which had by far the strongest effect on the species in this study were latitude and month (table 2. 1.). All gull species (figs. 2.2-2.6) and Starlings (fig. 2.7) were strongly affected by seasonal variation. All of these species peaked during the winter (fig. 2.11), with the exception of the Lesser Black-backed Gull, which reached a peak in numbers during the autumn. The effect of season was mitigated by an indirect effect acting through photoperiod. This accounted for most of the seasonal variation observed in the Herring Gull (fig. 2.2), and a large proportion in the Black Headed Gull (fig. 2.3), Lesser Black-backed Gull (fig. 2.5), Great Black-backed gull (fig. 2.6) and Starling (fig. 2.7). However, a proportion of the seasonal variation in the Black Headed Gull, Lesser Black-backed Gull, Great Black-backed Gull and Starling remained unexplained, and in the Common Gull little, if any of the seasonal variation was explained (table 2. 1.).

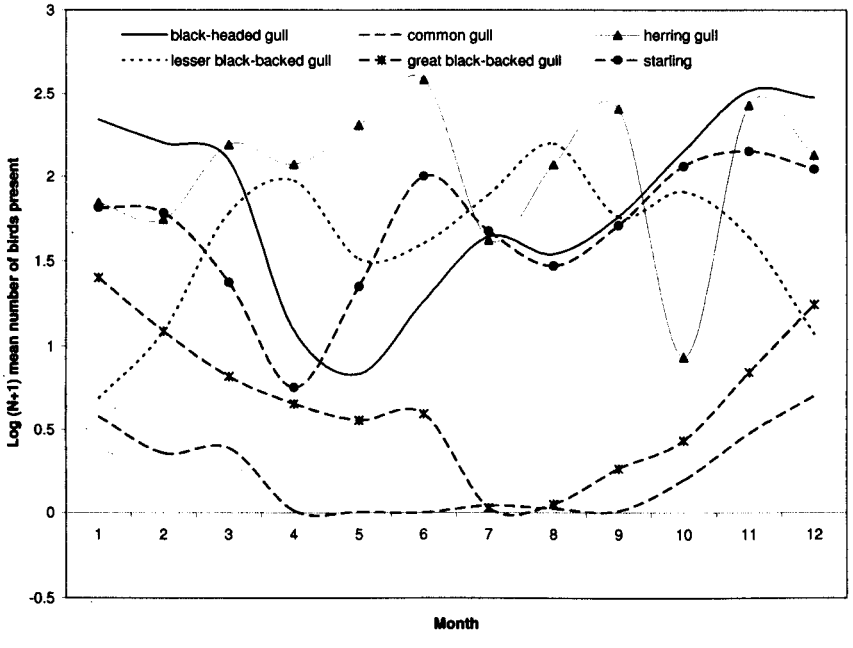


Figure 2. 11 Mean monthly variation in gull and starling numbers on landfill sites

The coefficients for sites indicates that the Herring Gull (fig. 2.2), Great Black-backed Gull (fig. 2.6) and Starling (fig. 2.7) were also strongly affected by site specific

differences, as were the Carrion Crow (fig. 2.8) and the Rook (fig. 2.9). Since much of this variation is unexplained by the indirect effects (table 2. 1.) of weather and human activity, this site specific variation is likely to be the result of unmeasured covariates, such as surrounding habitat in the landscape.

Whilst there were no site specific differences in the tipping regime, there were strong site specific differences in the application of control measures. However, due to the highly unbalanced nature of the data, it was not possible to compare individual techniques. Control and tipping were both affected by the day of the week, with both less likely to occur during the weekend, and both declined in their frequency throughout the three years of the study. The coefficients indicate that control increased in frequency during the winter and tipping increased in frequency with shorter photoperiod (figs. 2.3-2.6 and 2.8-2.10).

The sign of the coefficients for tipping activity showed that it attracted black-headed gulls, common gulls and lesser black-backed gulls, but deterred jackdaws (figs 2.3, 2.4, 2.5 and 2.10 and table 2.1). However, the responses of the black-headed gull and jackdaw were far stronger than those of the lesser black-backed or common gulls. Similarly, the application of control techniques caused significant declines in the common, lesser black-backed, great black-backed and gulls, as well as in the jackdaw (figs. 2.4, 2.5, 2.6 and 2.10). However, it had the opposite effect in the Carrion Crow and Rook (figs 2.8 and 2.9), strongly attracting both species.

There is a large amount of variation in the size of the U path coefficients, which quantify the amount of variation not explained by the models. These varied with species from 0.808 for black-headed gulls to 0.953 for jackdaws. This variation occurs due to missing covariates not measured during the original study. By considering each species together,

the size of the U path coefficient is correlated with the total effect size for month ($F_{1,7}$=5.669, P=0.048). This means that the amount of variation explained was affected by seasonal variation, and that more of the variation in the final models for species was explained for those species most prevalent in the winter.

Discussion

The management of species and their populations is an issue frequently faced by ecologists. This applies both to species which are rare or threatened that we wish to conserve and also to those which are pests that we wish to control. The success of these strategies has often been hampered by a lack of understanding of the systems involved. Attempts to control abundant species, such as the yellow-legged gull, *Larus cachinnans*, and great cormorant, *Phalcocorax carbo sinensis*, which can have major impacts on both the environment and on industry have had limited success (Bosch *et al.* 2000; Frederiksen *et al* 2001). This is due to a failure to account for the effects of population processes like emigration and density dependence.

The access to a reliable food supply is important to ensure both the survival (Acquarone *et al.* 2002; Schoech *et al.* 2007) and reproductive success of a range of species (Pons & Migot 1995; Massemin-Challet *et al.* 2006). Consequently, feeding stations, which provide a highly localised and predictable 2. source of food, often play an important part in the management plans for the conservation of rare or threatened birds such as the red kite, *Milvus milvus,* (Carter & Grice 2002), the griffon vulture, *Gyps fulvus,* (Bose & Sarrazin 2007) and the kakapo, *Strigops habroptilus*, (Powlesland & Lloyd 1994). However, some human activities, such as the creation of landfill sites, create feeding stations for non-desirable species which become focal points for pests. The extent to

which landfill sites are used by scavenging birds is dependent on a range of variables that are clearly correlated and interdependent. Whilst a number of studies have examined landfill use by birds, most have tended to focus on individual aspects of behaviour, typically spatial (Duhem *et al.* 2003) or temporal variation (Karlsson 2003). By using SEM it was possible to measure and quantify the relative importance of a series of interacting variables including space, time, weather and human activity.

In this study, seasonal processes and spatial variation were identified as the most important factors influencing bird abundance on landfill sites, however, this importance varied between species. The herring gull, great black-backed gull, rook, carrion crow and starling all exhibited strong spatial variation. Many species which exploit human garbage for food do so only when they are in close proximity to humans (Contesse *et al.* 2003; Mennechez & Clergeau 2006; Morey *et al.* 2006), suggesting that some factors other than food availability, such as habitat in the surrounding landscape, are influencing the spatial variation in these species use of garbage.

Gull species appear to seek out landfill sites and some have actually altered their range sizes in response to increased landfill availability (Horton *et al.* 1983). Their abundance on landfill sites may be limited only by landfill size (Sibly & McCleery1983; Sol *et al.* 1995). Given this, at first glance the spatial variation in landfill use observed in the great black-backed gull and herring gull may seem counter intuitive. For differing reasons, both species may be more likely to feed on landfill sites close to their roosts. The great-black backed gull is less likely than other gull species to utilise anthropogenic food (Wells 1994), suggesting that like the rook and carrion crow, its use of landfill sites may be opportunistic. The herring gull in contrast, is a highly aggressive and competitive species. As a result, it often out-competes other species feeding on landfill sites and is therefore

able to feed on those closest to its roost sites (Sibly & McCleery 1983; Kim & Monaghan 2006). There is competition both within and between gull species for access to food. Male herring gulls often occupy areas with access to the "freshest" waste that are also undisturbed by the actions of heavy vehicles, like refuse lorries and bulldozers (Greig *et al.* 1985), fiercly defending these areas from competitors. The black-headed gull is smaller and more agile than the herring gull and therefore able to forage closer to the heavy vehicles, avoiding the larger, more aggressive species (Bellbaum 2005)

In contrast to corvid species, starlings and gull species all showed a pronounced seasonality in their tendency to use landfill sites, with an increased abundance during the winter. The combined effects of lower temperatures (Chamberlain *et al.* 2005), reduced photoperiod (Polo *et al.* 2007) and reduced food availability (Robinson *et al.* 2007) during the winter make it harder for bird to make sufficient daily energy gains during the winter. Consequently, many species alter their foraging behaviour to compensate, often relying more heavily on the supplementary food provided by feeding stations. Life history phenomena related to breeding and migration patterns may also contribute to the increase in abundance of some species seen at landfill sites during the winter. There is evidence of a shift in the diet of gulls during the breeding season. The health of chicks fed "non-natural" food, such as garbage, is often adversely affected (Murphy *et al.* 1984; Pierroti & Annett 1991; Belant *et al.* 1993; Mennechez & Clergeau 2006). Consequently, during the breeding season adults often forage around fishery discards and trawlers, where they can access "higher quality" food such as fish (Furness *et al.* 1992; Belant *et al.* 1993), before returning to forage on more reliable sources of food, such as landfill sites during the winter. The density of gulls feeding on landfill sites is likely to be further increased during the winter as resident populations are supplemented with large numbers of migrants (Wernham *et al.* 2002).

Whilst we were able to identify important underlying trends in the data, the U path coefficients of our models indicate that there was still a sizeable proportion of the variation in abundance we were unable to explain. Previous studies have cited factors such as the availability of alternative sources of food and competitive behaviour as important in determining avian abundance on landfill sites (Sibly & McCleary 1983; Coulson 1987; Bellebaum 2005) however, in this study it was not possible to account for these. The analysis of the U coefficients by species suggests that migratory behaviour may be an important factor in predicting the abundance of scavenging birds on landfill sites. It was easier to explain variation in species such as the gulls, whose presence on landfill sites peaks during the winter, than it was for species whose presence was more consistent throughout the year. This suggests that some species, such as the jackdaw, may be responding to more subtle changes in the local environment that were not measured during this study.

The spatial and seasonal variation observed in bird abundance at landfill sites mean that a "one size fits all" strategy for managing problem species is unlikely to be either cost effective or successful. In the past, strategies to deal with problem bird populations have included targeted culling (Harris & Wanless 1997; Guillemette & Brousseau 2001; Oro & Martinez-Abrain 2007), bird harassment regimes (ie Cook *et al.* 2008) and on landfill sites, alterations to waste management practices (ie Belant 1997; Burger 2001). In the short term, culling is often effective (i.e Harris & Wanless 1997), however, due to population dispersal and the need for constant reinforcement, in the long term it is often ineffective (Oro & Martinez-Abrain 2007). Therefore, whilst it may prove effective in reducing populations of sedentary species, such as corvids, until more is understood about the winter site fidelity of migratory species, like gulls, it cannot be recommended for wider use.

The effectiveness of bird harassment regimes is highly variable, and is often dependent on the techniques used (Gilsdorf *et al.* 2002; Cook *et al.* 2008). Many of these techniques are both expensive to implement and also subject to habituation. Consequently, they are often only of use for a limited time frame, suggesting that will they be most effective when targeted to periods when pest species are in their greatest abundance.

Reducing access to waste has proven to be effective at reducing problem bird numbers (Belant 1997; Burger 2001; Soh *et al.* 2002). As gulls distribute themselves in proportion to landfill size (Sibly & McCleery 1983; Sol *et al.* 1995), reducing waste availability by tipping at night, when fewer birds are present, or covering fresh waste more quickly may be an effective method for reducing the abundance of problem species on landfill sites. This, in combination with the use of harassment regimes during periods of peak abundance, such as the winter, may reduce the problem of pest species on landfill sites.

By using SEM we have been able to identify and quantify spatial and temporal effects on species using landfill sites. This allows the development of targeted management strategies. Furthermore, this study demonstrates the utility of SEM in analysing complex datasets containing series of correlated variables. The absence of such a technique has limited the field of ecology (Grace 2006). Tools which allow us to analyse complex ecological systems are vital in the development of management strategies, whether for the control of pest species or the conservation of threatened ones.

Chapter 3: A comparison of winter and summer habitat preferences of gulls in England and Wales

Abstract

In recent years there have been two major studies of gull distribution in the UK, the Joint Nature Consultancy Committee's (JNCC) seabird 2000 census of breeding colonies and the British Trust for Ornithology's (BTO) Winter Gull roost survey. We use the results of these surveys to investigate factors influencing the summer and winter distribution of gulls. Investigations of species distributions underpin much ecological and conservation research. However, these are often hampered by the effects of spatial autocorrelation. We use three modelling strategies, autocovariate regression, negative binomial generalised linear models (GLMs) and generalised least squares, that account for spatial autocorrelation to investigate the spatial distribution of gulls and compare their efficacy. The negative binomial models proved the most effective as they include a dispersion parameter, theta (θ), that can account for the aggregation of roosts. During the winter, gulls demonstrated a preference for warm, inland areas. During the summer, a strong preference was shown for coastal areas with a reliable food supply, such as fishing ports. The models for the summer distribution of gulls produced better levels of fit than those for the winter distribution. This implies that habitat choices of gulls are more constrained during the summer when they are provisioning for chicks than during the winter.

Introduction

In contrast to much of the nations avifauna (i.e. Pain *et al.* 1997; van den Berg *et al.* 2001; Lilley & Clarke 2003; Devictor *et al.* 2007), many gull species have dramatically expanded their ranges in response to human modifications of the landscape. Increasing urbanisation has provided new nesting opportunities for gulls on roof tops (Monaghan &

Coulson 1978; Monaghan 1979: Raven & Coulson 1997; Mitchell *et al.* 2004), and the concentration of large quantities of waste in landfill sites has provided them with a new, superabundant food source to exploit (Horton *et al.* 1983; Burton *et al.* 2002; Duhem *et al.* 2007). This range expansion has brought with it a number of problems that have serious economic implications and threatens the health of both humans and domestic animals. Gulls are often present in large aggregations, which can cause a great deal of damage to town centres, and their aggressive nature makes them a general nuisance (Vermeer *et al.* 1988; Belant 1997). These large aggregations also pose a risk to air safety (Dolbeer *et al.* 1993), and gulls are involved in more collisions with military aircraft than any other species (Cleary *et al.* 2006). Finally, gulls carry a range of pathogens including, Salmonella (Kapperud & Rosef 1983; Ferns & Mudge 2000; Wahlstrom *et al.* 2003; Nesse *et al.* 2005; Palmgren *et al.* 2006; Cizek *et al.* 2007), Campylobacter (Kapperud & Rosef 1983; Broman *et al.* 2002) and E-Coli (Wallace *et al.* 1997; Fogarty *et al.* 2003; Nelson *et al.* 2008). Gulls often aggregate in areas, like playing fields and farmland, where they come into contact with humans on a daily basis (Cramp *et al.* 1983) risking the zoonotic transmission of these pathogens.

Consequently, a great deal of money has been invested in investigating measures to reduce the risks associated with large aggregations of gulls including, culling (Bosch *et al.* 2000), harassment (Cook *et al.* 2008; Soldatini *et al.* 2008) and egg oiling (Blokpoel & Hamilton 1989; Christens & Blokpoel 1991; Blackwell *et al.* 2000a). However, due to the need for the spatial coordination of these measures (Belant 1997), these have often been ineffective. In order to enable this greater spatial coordination, it is important to understand how gulls disperse throughout the landscape, and what features attract large aggregations.

These large aggregations mean that the distribution of gulls across the landscape is likely to be spatially autocorrelated. Spatial autocorrelation is the similarity of samples from neighbouring areas, which violates the assumptions of identically and independently distributed errors. This inflates the risks of a type 1 error, falsely rejecting the null hypothesis, by incorrectly estimating coefficients and their standard errors (Guisan *et al.*2006; Dormann 2007; Dormann *et al.* 2007). There are a wide variety of statistical techniques that can be used to account for spatial autocorrelation. We consider three of these techniques here, autocovariate regression, generalised least squares (GLS) and negative binomial generalised linear models (GLMs). By including an extra parameter based on the size of, and distance to, neighbouring sites, autocovariate regression is able to account for spatial autocorrelation resulting from processes like conspecific attraction and dispersal (Dormann *et al.* 2007). In contrast, generalised least squares (GLS) directly models any spatial autocorrelation by incorporating a spatial covariance structure in the variance-covariance matrix (Pinheiro & Bates 2000).

The negative binomial error structure has long been proposed as a mechanism to explain the distribution of animals within the environment, able to describe processes such as dispersal (Binns 1986). This distribution assumes that there is an initial, Poisson distributed invasion in to an area. Following this invasion, each individual has a probability of "disappearing" (through processes such as migration or mortality). The individuals that remain are able to reproduce, and adopt a logarithmic distribution (Binns 1986). By fitting a GLM with a negative binomial error structure, a dispersion parameter, theta (θ), is included which accounts for the aggregated nature of many organisms populations (Venables & Ripley 2002).

In addition to the effects of spatial autocorrelation, analysis of the distribution of gull species is complicated by aspects of their ecology. Any analysis of how the landscape influences the distribution of gull species must be done at an appropriate scale. Gulls are generalist feeders capable of travelling long distances every day (Cramp *et al.*1983). This makes it difficult to define a scale at which to investigate the landscape level effects of habitat. In addition, their migratory nature (Wernham *et al.* 2002) suggests that they are likely to respond differently to their environment during the breeding season and over winter. Consequently, in order to build a picture of how gulls use the landscape, it is necessary to consider both their summer and winter distribution. We investigate how habitat, weather and human activity combine to affect the size and distribution of gull roosts and breeding sites. We then discuss how the differences in the summer and winter distribution of gulls arise. Previous studies focussed on habitat preferences in breeding season (i.e. Fasola & Canova 1992; Bosch & Sol 1998) and have often failed to take account of spatial autocorrelation.

Methodology

Data collection

Data comprise counts of the number of the number of herring, black-headed, lesser black-backed and great black backed gulls present on winter and summer roost sites throughout England and Wales. Winter data were obtained from the British Trust for Ornithology's (BTO's) 2003 Winter Gull Roost Survey (WinGS) of 863 sites in England and Wales. Summer data were obtained from counts of breeding pairs at 533 roost sites as part of the Joint Nature Conservancy Council's (JNCC's) Seabird 2000 survey. Sites from Scotland were excluded from our analysis due to poorer coverage.

Collation of covariates

Covariates were collected from a variety of sources. Rainfall and temperatures were not available for each roost, so we obtained them from 1971-2000 averages from the nearest weather station (Met Office 2008). Long term averages were used for weather variables rather than data from the relevant years as the largest gull roosts are likely to have been in place over a long time period, and therefore to have responded to an areas "average" climate rather than its climate at any given point in time. These stations were a mean distance of 4.2 km (± 0.2 km S.E.) from winter roosts and 34.1 km (± 0.1 km S.E.) from summer roosts. Sea surface temperature averages were obtained from monitoring stations with a mean distance of 5.4 km (±0.2 km S.E.) from winter roosts and 43.9 km (± 0.5 km S.E.) from summer roosts (CEFAS 2008). It was hypothesised that despite their ability to forage over wide areas, gulls would seek to minimise their energetic costs by roosting and breeding close to reliable sources of food. Consequently, distance to landfill sites and fishing ports were included in the models, the total annual catch landed at each port was also included as it was hypothesised that larger ports would be more attractive to gulls. Landfill site locations were obtained from the Environment Agency's REGIS database, whilst port size (the total annual catch landed at each port) and locations came from DEFRA.

Since we were interested in ascertaining the potential role of the surrounding habitat in determining the population size of each roost at a scale that was relevant to the gulls, we collated habitat information at five scales, 0.5 km^2, 5 km^2, 10 km^2, 20 km^2 and 30 km^2, from the roost centre. Data were obtained from the UK Land Cover Map (CEH 2000) using the GRASS 5.4.0 GIS package. The values obtained for the surrounding 0.5km^2 were subtracted from each of the other areas so that the effects of local versus landscape habitat could be considered. For each area, the habitat variables were then summarised to

two axes using detrended correspondence analysis (DCA) in the vegan extension (Oksanen *et al.* 2007) of R 2.6.2 (R core development team 2008). Finally, the altitude of each site was obtained using the UK digital terrain map. At a local scale we hypothesised that gulls would select areas which were sheltered and free from disturbance, whilst at the landscape scale they would select areas that provided easy access to a reliable source of food.

Data analysis

We used autocovariate regression, Generalised Least Squares (GLS) models and Generalised Linear Models (GLMs) with a negative binomial error structure to investigate factors affecting the distribution and size of gull roost sites. We first used simple GLMs to identify putative covariates affecting the size of roosts and removing those that were not significant. The aggregation observed in gull populations is likely to lead to serial dependency in the model residuals, which can severely affect both coefficient estimates and overall model fit (Dormann 2007). By creating a spatial autocovariate, which weights each roost according to the size and proximity of surrounding roosts, using the R extension spdep (Bivand *et al.* 2007), it is possible to account for this aggregation. By introducing this into our initial GLM, we create an autocovariate regression.

Following this, we fit a GLM with a negative binomial error structure, using the R extension MASS (Venables & Ripley 2002). These models include a measure of aggregation, theta (θ), and we again include the spatial autocovariate this time to investigate to effect of surrounding populations on the size of our roost sites. Finally, we used Generalised Least Squares (GLS) models in the R extension nlme (Pinheiro *et al.* 2006) which allows us to directly model the effects of spatial autocorrelation by including

a variance-covariance matrix. For this, we base the variance covariance matrix on the ranked autocovariate.

For each model, a similar strategy was adopted to decide which variables warranted inclusion in a final, parsimonious model. Initially, four simple models were constructed to compare the effects of the 5, 10, 20 and 30 km ^{2} habitat ordinations. The area which produced the lowest model AIC was then included in the full model. The full models were then fitted, and variables dropped using likelihood ratio tests to compare AIC values, until a parsimonious model remained.

Results

Initial exploratory analysis revealed spatial autocorrelation in the size of gull roosts. As a failure to account for this autocorrelation can lead to an inaccurate estimate of coefficients (Dormann *et al.* 2007), we must consider strategies that can take this into account. The different error structures of our modelling strategies meant that it was not possible to use traditional measures, like Aikaike's Information Criterion (AIC), to compare between models. Instead, we used a crude measure of model fit, deviance explained (D^2). We found that overall, the GLS models performed poorly, often explaining far less variation

	Summer						Winter					
	GLM		Negative Binomial		GLS		GLM		Negative Binomial		GLS	
	Coeff.	P	Coeff.	P	Coeff.	P	Coeff.	P	Coeff.	P	Coeff.	P
Intercept	0.911	<0.001	3.247	<0.001	1.181	<0.001	2.524	0.012	2.524	0.012	1.892	<0.001
Easting	$7x10^{-7}$	0.021										
Northing	$1x10^{-6}$	<0.001	$4x10^{-6}$	<0.001	$1x10^{-6}$	<0.001	$6x10^{-7}$	0.017				
Autocovariate			0.680	0.002			0.003	0.011	0.755	0.003		
Dist. to port	-0.024	0.001	-0.045	0.016								
Port size	-0.087	0.1035	-0.328	0.003								
Dist. to port *port size	0.008	0.005	0.021	0.002								
Dist. to breeding /winter site			-0.017	0.016								
Rain	0.001	0.031										
Min. Temp.									-0.477	<0.001		
Max. Temp.									0.388	0.005		
20 km² DCA1	-0.246	0.003	-0.624	0.001	-0.196	0.013	-0.373	<0.001			0.241	0.010
20 km² DCA2	-0.392	0.023	-0.738	0.021			-0.369	0.001	-0.719	0.001	-0.319	0.009
AIC	561		3159		612		964		5254		1015	
D^2	0.188		0.396		0.114		0.105		0.065		0.037	
Residual Deviance	106 on 291 D. F.		360 on 291 D. F.		116 on 297 D. F.		253 on 395 D. F.		518 on 395 D. F.		285 on 400 D. F.	

Table 3.1 Parsimonious GLM, Negative Binomial GLM and GLS models for summer breeding site and winter roost site sizes in the herring gull. Also reported are the values for Aikaike's Information Criterion (AIC), Deviance Explained (D^2) and Residual Deviance for each model.

	Summer						Winter					
	GLM		Negative Binomial		GLS		GLM		Negative Binomial		GLS	
	Coeff.	P	Coeff.	P	Coeff.	P	Coeff.	P	Coeff.	P	Coeff.	P
Intercept	-4.370	0.004	1.529	0.018	-4.359	0.004	-0.463	0.217	-1.873	0.027	-0.037	0.927
Northing	$4x10^{-6}$	<0.001	$6x10^{-6}$	<0.001	$2x10^{-6}$	<0.001			$2x10^{-6}$	<0.001		
Autocovariate			1.821	<0.001			0.719	<0.001	1.800	<0.001		
Dist. to port			-0.065	0.007								
Port size			-2.985	0.1416								
Dist. to port *port size			0.037	<0.001								
Dist. to breeding /winter site			0.007	0.519					-0.019	0.032		
Breeding/winter site size			0.183	0.428			-0.103	0.048	-0.294	0.007		
Dist. to breeding /winter site*size			-0.043	<0.001								
Altitude									-0.006	0.002		
Sea Surface Temperature							0.100	0.017	0.561	<0.001	0.149	0.001
Max. Temp.	0.297	0.006			0.297	<0.001						
0.5 km² DCA 1			-0.334	0.014			0.091	0.014	0.612	<0.001		
20 km² DCA1	-0.488	<0.001			-0.487	<0.001						
20 km² DCA2	-0.699	0.003	-3.081	<0.001	-0.696	0.003						
30 km² DCA1											-0.580	<0.001
30 km² DCA2									0.648	0.034		
AIC	479		1848		519		595		2657		651	
D^2	0.149		0.422		0.149		0.287		0.287		0.143	
Residual Deviance	137 on 178 D. F.		242 on 172 D. F.		137 on 178 D. F.		142 on 257 D. F.		326 on 252 D. F.		170 on 259 D. F.	

Table 3.2 Parsimonious GLM, Negative Binomial GLM and GLS models for summer breeding site and winter roost site sizes in the lesser black backed gull. Also reported are the values for Aikaike's Information Criterion (AIC), Deviance Explained (D^2) and Residual Deviance for each model.

	Summer						Winter					
	GLM		Negative Binomial		GLS		GLM		Negative Binomial		GLS	
	Coeff.	P	Coeff.	P	Coeff.	P	Coeff.	P	Coeff.	P	Coeff.	P
Intercept	2.984	<0.001	12.886	<0.001	3.491	<0.001	0.237	0.069	-1.352	0.032	1.131	<0.001
Easting									$3x10^{-6}$	<0.001		
Autocovariate							0.743	<0.001	1.744	<0.001		
Dist. to port									0.075	0.006		
Port size	0.092	0.061										
Dist. to breeding /winter site			-0.012	0.030			0.008	0.025				
Altitude									0.008	<0.001	0.003	<0.001
Sea Surface Temperature	-0.184	<0.001	-0.833	<0.001	-0.207	<0.001			0.014	<0.001		
0.5 km² DCA 1	-0.106	0.058	-0.364	0.016								
5 km² DCA2			2.450	<0.001	0.480	0.008					-0.665	<0.001
30 km² DCA2									-1.542	<0.001		
AIC	167		834		177		598		2829		644	
D^2	0.205		0.364		0.199		0.179		0.268		0.092	
Residual Deviance	25 on121 D. F.		131 on 120 D. F.		25 on 122 D. F.		127 on 292 D. F.		361 on 288 D. F.		141 on 292 D. F.	

Table 3.3 Parsimonious GLM, Negative Binomial GLM and GLS models for summer breeding site and winter roost site sizes in the great black backed gull. Also reported are the values for Aikaike's Information Criterion (AIC), Deviance Explained (D^2) and Residual Deviance for each model.

	Summer						Winter					
	GLM		Negative Binomial		GLS		GLM		Negative Binomial		GLS	
	Coeff.	P	Coeff.	P	Coeff.	P	Coeff.	P	Coeff.	P	Coeff.	P
Intercept	4.32	<0.001	14.54	<0.001	2.24	<0.001	1.49	<0.001	3.48	<0.001	2.77	<0.001
Autocovariate							0.50	<0.001	1.01	<0.001		
Dist. to landfill	-0.01	0.027	-0.05	<0.001			-0.01	0.030	-0.01	0.018	-0.01	<0.001
Dist. to port	-0.01	0.026	-0.06	<0.001	-0.01	0.003			0.05	0.009		
Port size			-0.52	0.015								
Dist. to port *port size			0.02	<0.001								
Dist. to breeding /winter site	0.05	0.059							0.02	0.014	0.010	0.004
Winter site size	0.20	0.041										
Dist. to breeding /winter site*site size	-0.02	0.029										
Altitude							-0.01	0.027	-0.01	0.001		
Maximum Temperature	-0.14	0.039	-0.37	0.005								
Sea Surface Temperature									0.12	0.037		
0.5 km² DCA1	-0.27	0.022	-1.12	<0.001								
0.5 km² DCA2									0.36	0.005		
5 km² DCA1			0.64	0.022								
5 km² DCA2			1.09	0.013	0.55	0.028						
30 km² DCA1							-0.48	<0.001	-1.10	<0.001	-0.70	<0.001
AIC	344		1683		362		966		7185		1012	
D^2	0.206		0.368		0.130		0.317		0.297		0.283	
Residual Deviance	89 on 126 D. F.		169 on 125 D. F.		97 on 131 D. F.		228 on 430 D. F.		532 on 426 D. F.		239 on 435 D. F.	

Table 3.4 Parsimonious GLM, Negative Binomial GLM and GLS models for summer breeding site and winter roost site sizes in the black-headed gull. Also reported are the values for Aikaike's Information Criterion (AIC), Deviance Explained (D^2) and Residual Deviance for each model.

	Summer	Winter
Black-headed gull	0.449 (±0.045)	0.619 (±0.035)
Herring Gull	0.618 (±0.043)	0.399 (±0.023)
Lesser Black-backed Gull	0.324 (±0.024)	0.424 (±0.031)
Great Black-backed Gull	0.936 (±0.120)	0.479 (±0.033)

Table 3.5 Values of theta (θ) (± Standard Error) for each species summer and winter negative binomial GLM. As Theta $\rightarrow \infty$ the degree of aggregation decreases

overall than either autocovariate regression or negative binomial GLMs (Tables 3.1-3.4). The negative binomial models explained similar or greater levels of variation than the autocovariate regression, and identified a greater number of significant explanatory variables than either other method (Tables 3.1-3.4). Values of θ from the negative binomial GLMs revealed a high degree of aggregation amongst gull roosts (Table 3.5), however, there was no significant difference in aggregation between summer and winter ($t = 0.697$; $p = 0.536$). Further support for the use of negative binomial GLMs came from the over dispersed nature of their residuals. Unless otherwise stated all subsequent results refer to the negative binomial models.

Distribution of gulls during the winter

During the winter, the predicted distribution of gulls matched the observed distribution closely, with the exception of the herring gull (Figures 3.1-3.4). There was no evidence of a spatial pattern to the residuals. The gulls were widely distributed, often present inland in large numbers. All roosts were highly aggregated (Table 3.5), and the effects of the autocovariate indicate that the largest roosts tended to be closest together (Tables 3.1-3.4). Proximity to summer roosts significantly increased the size of lesser black-backed gulls, whilst it decreased the size of black-headed gull roosts, and the autocovariate regression indicated a similar relationship in the great black-backed gull. The largest roosts of the lesser black-backed gulls had a northerly distribution and the largest great black-backed gulls had an easterly distribution. A northerly distribution was also indicated in the

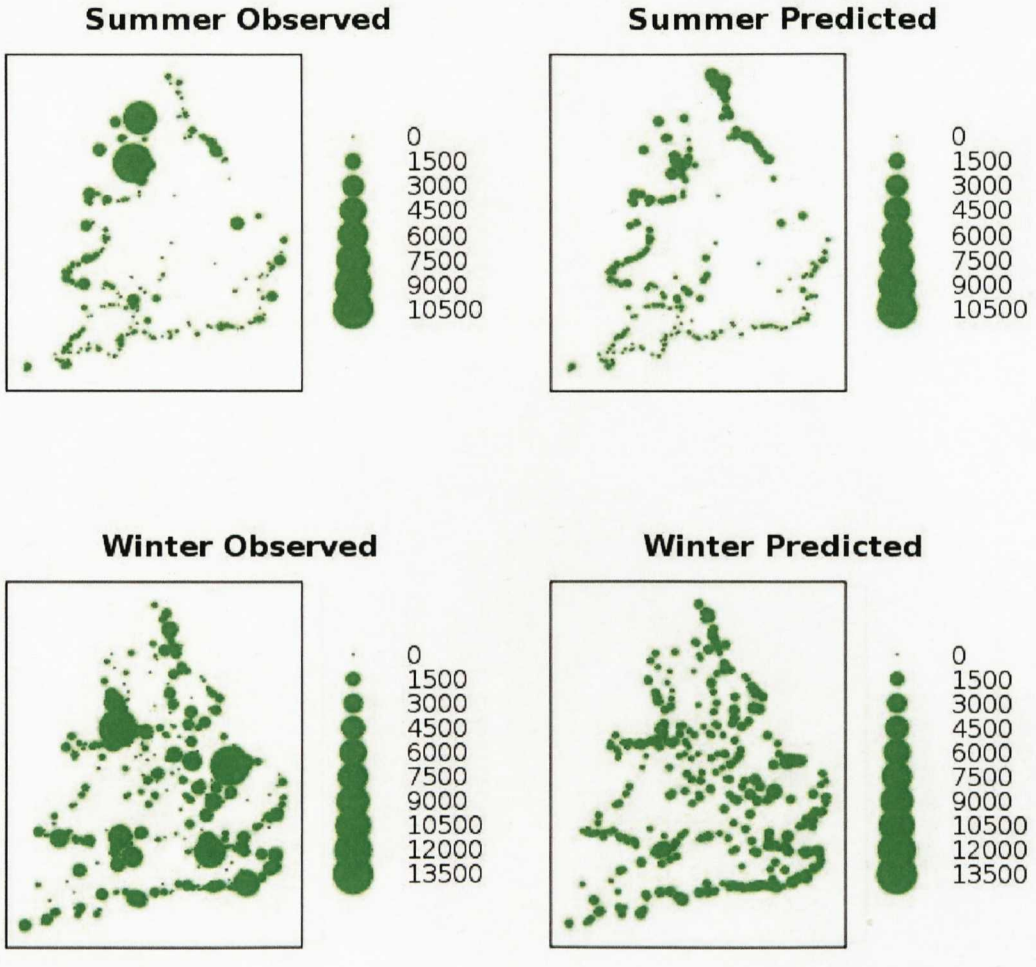


Figure 3.1 Observed and predicted distributions of the herring gull during the summer and winter, predicted distribution from the fitted values of negative binomial generalised linear models.

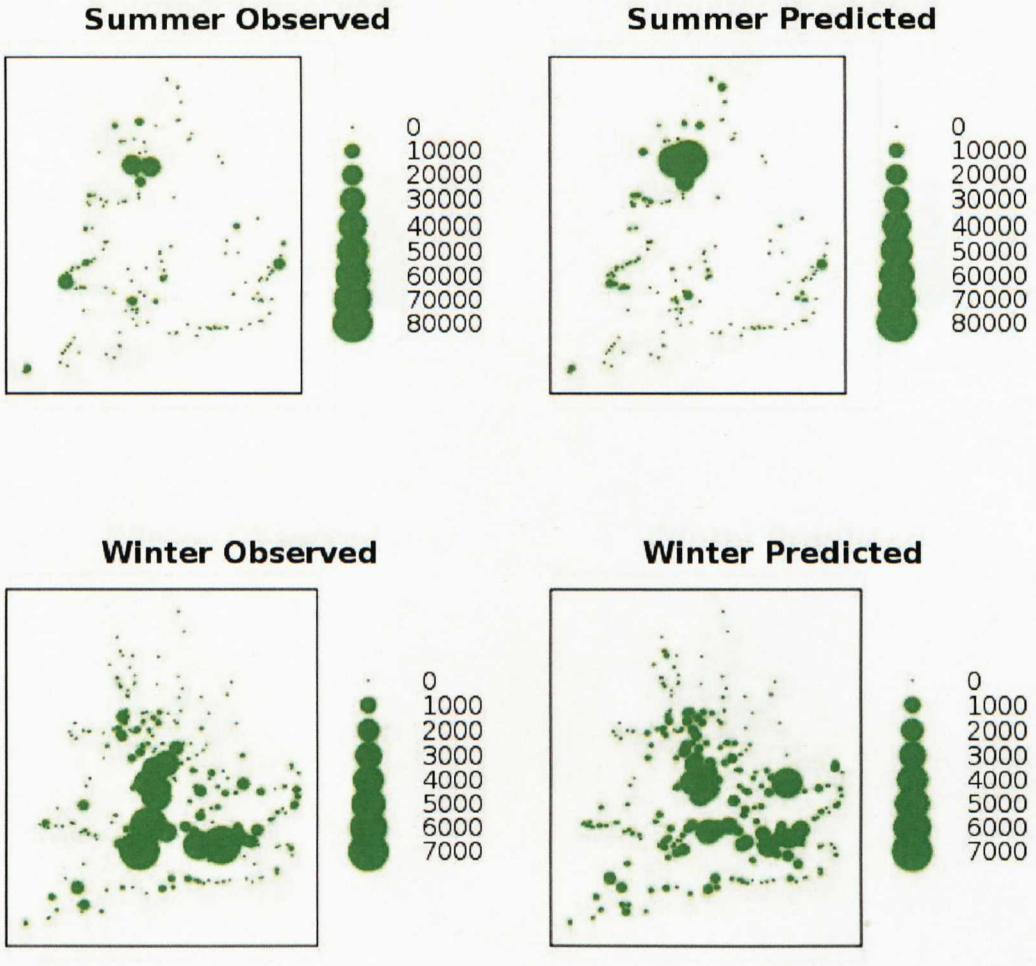


Figure 3.2 Observed and predicted distributions of the lesser black-backed gull during the summer and winter, predicted distribution from the fitted values of negative binomial generalised linear models.

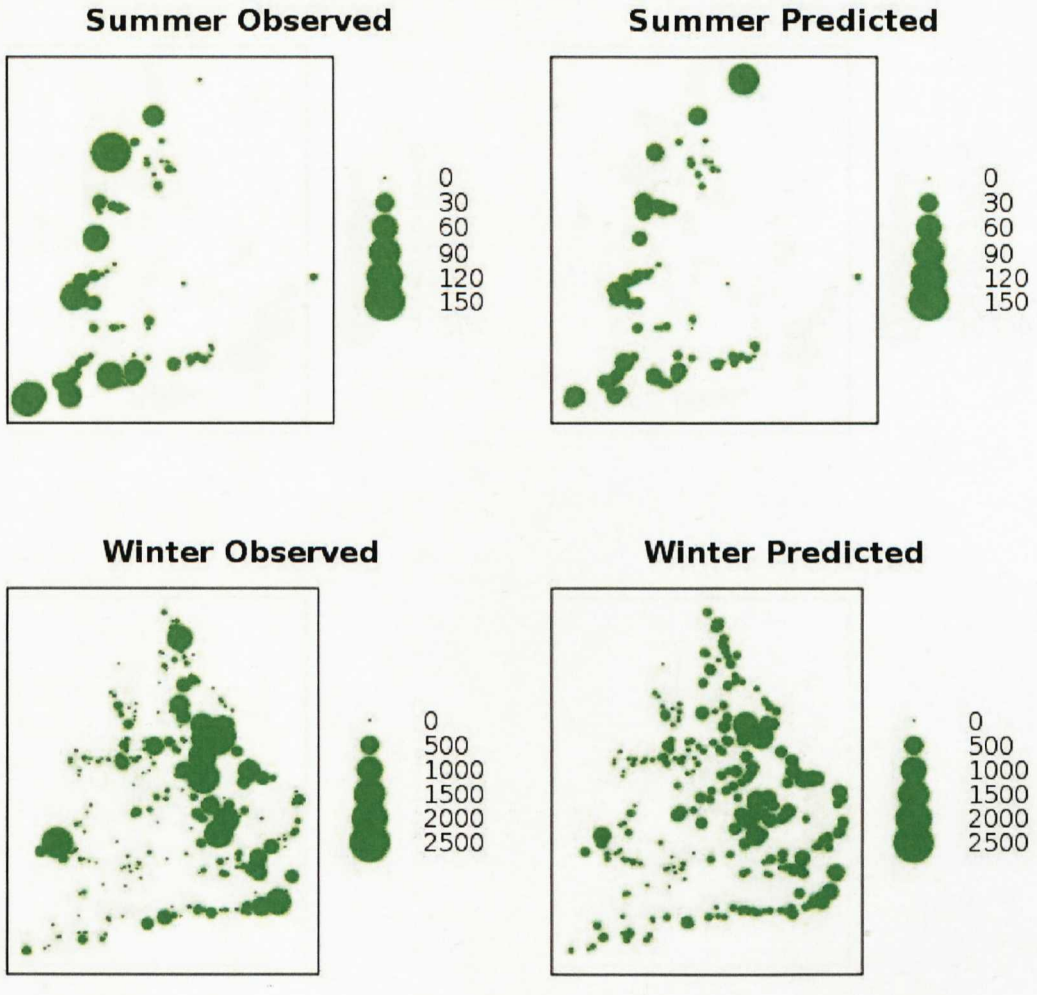


Figure 3.3 Observed and predicted distributions of the great black-backed gull during the summer and winter, predicted distribution from the fitted values of negative binomial generalised linear models.

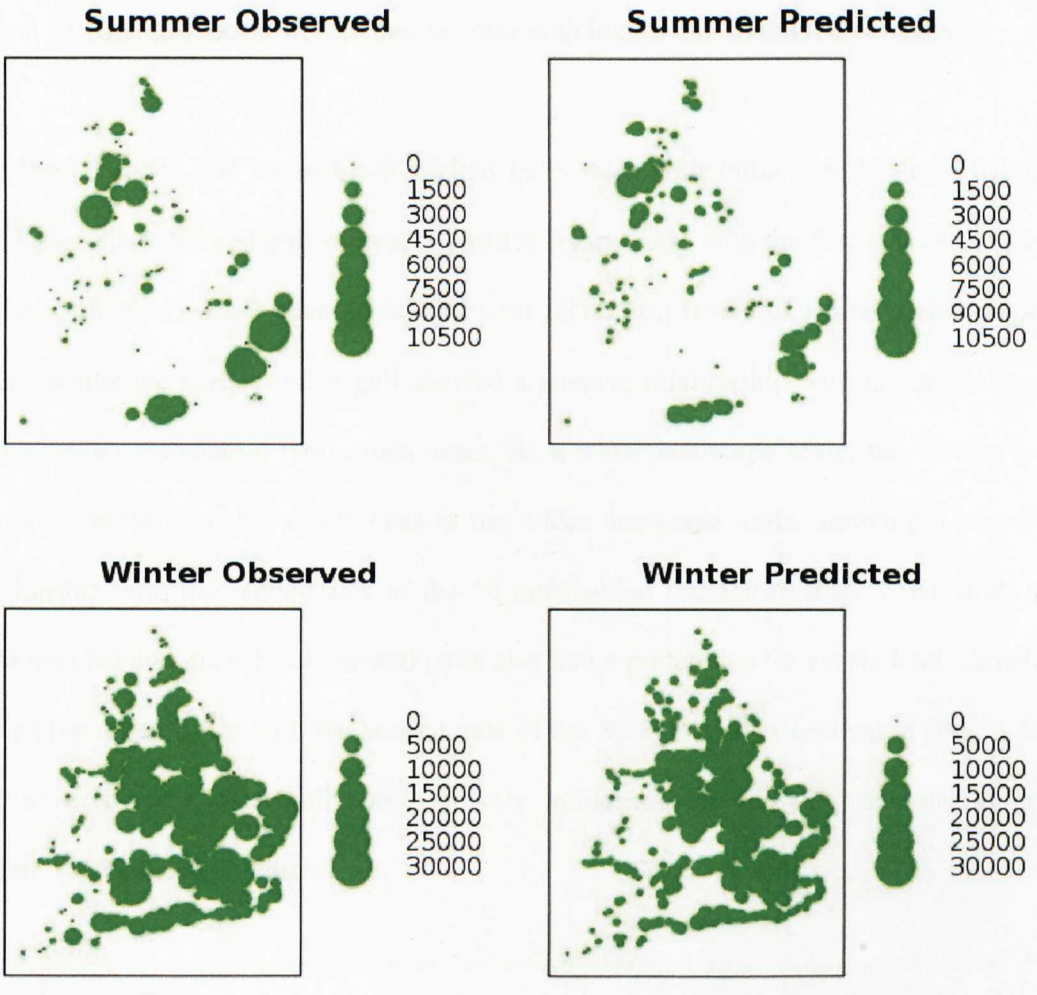


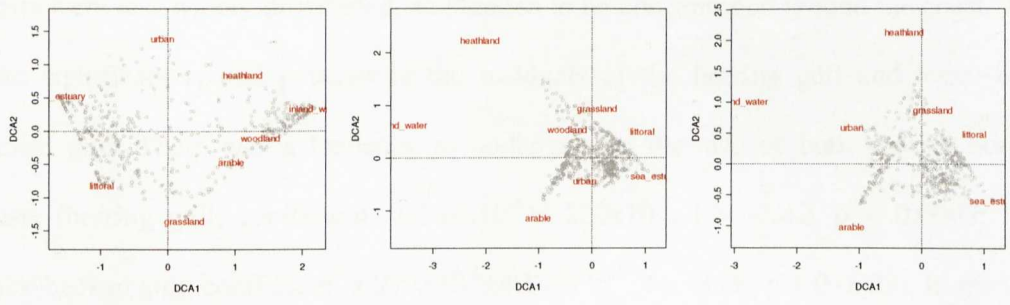
Figure 3.4 Observed and predicted distributions of the black-headed gull during the summer and winter, predicted distribution from the fitted values of negative binomial generalised linear models.

herring gull by autocovariate regression. All three modelling approaches show that the largest roosts of the black-headed gull were located close to landfill sites. This relationship was not repeated in any of the other species. The largest roosts of both the black-headed gull and lesser black-backed gull were found away from ports.

Temperature played an important role in determining the observed winter roost sizes (Tables 3.1-3.4). The largest lesser black-backed, great black-backed and black-headed

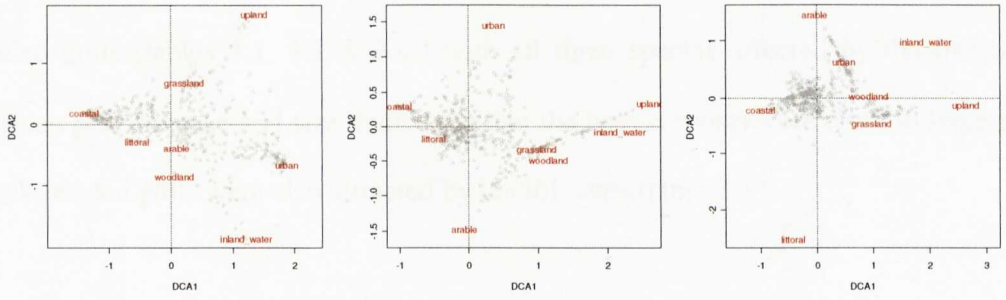
gull roosts were all found close to areas with high sea surface temperatures, whilst the largest herring gull roosts were found in areas with higher maximum temperatures.

The black headed and lesser black-backed gulls were both influenced by local habitat. The lesser black-backed gull showed a positive relationship with the first axis of the local habitat ordination which was associated with increasing levels of inland water (Figure 3.5.a), whilst the black-headed gull showed a positive relationship with the second axis, indicating an association with urban areas. At a wider landscape scale, the herring gull showed a preference for arable land at the wider landscape scale, showing a negative relationship with the second axis of the 20 km² habitat ordination (Fig. 3.5b). Both the black-headed and great black-backed gulls also had a preference for arable land, showing a negative relationship with the second axis of the 30 km² habitat ordination (Fig. 3.5c). The lesser black backed gull was positively influenced by this axis, demonstrating a preference for heath and grassland.



(a) (b) (c)

Figure 3.5 Detrended Corresponadance Analysis was used to categorise the habitat surrounding each of the winter roost sites by summarising data obtained from the CEH landcover map at different spatial scales. (a) at 0.5 km², the first axis represents a trend from estuarine to freshwater habitats, the second axis represents a trend from rural to urban habitats. (b) at 20 km², the first axis represnts a trend from freshwater to estuarine habitats and the second represents a trend from urban and arable habitats to more "natural" habitats. (c) at 30 km², the first axis represents a trend from freshwater to estuarine habitats and the second axis represents a trend from arable to less developed habitats.



(a) (b) (c)

Figure 3.6 Detrended Corresponadance Analysis was used to categorise the habitat surrounding each of the summer breeding sites by summarising data obtained from the CEH landcover map at different spatial scales. (a) at 0.5 km², the first axis represents a trend from coastal to urban habitats, the second axis represents a trend from rural to urban habitats. (b) at 5 km², the first axis represnts a trend from coastal to upland and freshwater habitats and the second represents a trend from arable to urban habitats. (c) at 20 km², the first axis represents a trend from coastal to upland habitats and the second axis represents a trend from arable to littoral habitats.

Distribution of gulls during the summer

For each species, the predicted distributions during the summer more closely matched the observed distributions than during the winter (Figures 3.1-3.4). In contrast to the winter roosts were less widely distributed, and tended to be concentrated around the coast. There were significant spatial patterns in the residuals of the herring gull and lesser-black-backed gull. There was a tendency to under-predict the size of both species northern roosts (herring gull, coefficient $-1.104 \times 10^{-6} \pm 3.220 \times 10^{-7}$, $t = -3.42$, $p = 0.0007$; lesser black-backed gull, coefficient $-1.277 \times 10^{-6} \pm 4.140 \times 10^{-7}$, $t = -3.08$, $p = 0.0023$). In the lesser black-backed gull there was also a tendency to over-predict the size of western roosts (coefficient $-1.209 \times 10^{-6} \pm 4.480 \times 10^{-7}$, $t = 2.69$, $p = 0.0076$). The spatial auto-covariate had a significant positive effect on the size of herring and lesser black backed gull breeding colonies, indicating that the largest sites tended to be closest together (tables 3.1 and 3.2; figures 3.1 and 3.2.). In addition, the largest herring gull roosts were located close to the winter roost sites, a trend shared with the great black-backed gull (table 3.3.).

Fishing ports were significant predictors for herring, lesser black-backed and black-headed gulls (tables 3.1, 3.2 & 3.4.) with all three species affected by the interaction between port distance and size, indicating that the largest roosts were close to large ports. Black-headed gulls were also attracted by landfill sites (table 3.4.).

There was some indication that cooler areas were preferred, with black-headed gulls present in larger numbers in areas with lower maximum temperatures (table 3.4.) and great black-backed gulls present in areas with lower sea surface temperatures (table 3.3.). In contrast, the autocovariate regression and GLS indicated that the largest lesser black-backed gull roosts were found in warmer areas (table 3.2.). Autocovariate regression also indicated that the larger herring gull roosts were located in areas with heavy rainfall (table 3.1.).

Local habitat was more important during the summer than during the winter with the largest black-headed, lesser black-backed and great black-backed gull roosts all associated with coastal habitats (tables 3.2-3.4; Fig. 3.6a) in the surrounding 0.5km^2. In the wider landscape all four species were influenced by habitat at a smaller scale than during the winter (5 km^2 in the case of the black-headed and great black-backed gulls, and 20 km^2 in the case of the herring and lesser black-backed gulls) (Tables 3.1-3.4). The great black-backed and black-headed gulls responded positively to the second axis of the 5 km^2 habitat ordination (tables 3.3 & 3.4; Fig. 3.6b) showing an association with areas of grass and heath land. The black-headed gull also responded positively to the first axis, associated with increasing urbanisation. The negative relationship with the first axis of the 20 km^2 habitat ordination indicated that herring gulls were associated with estuarine habitats, a relationship also identified by the autocovariate regression and GLS analysis in the lesser black-backed gull (tables 3.1 & 3.2; Fig. 3.6c). Both species were also

negatively influenced by the second axis of this ordination, showing an association with urban areas.

Discussion

The negative binomial distribution has long been proposed as a mechanism for describing the mean density, and its variability, of organisms as it allows for events such as dispersal, reproduction or death that can be influenced by environmental conditions (Binns 1986; White & Bennetts 1996). We found that they were the most effective analytical technique for investigating the distribution of summer and winter gull roosts. Auto-covariate regression, our standard GLMs, can misrepresent the importance of explanatory variables (Dormann *et al.* 2007). The over dispersed residual deviance and low values of θ also support the use of a negative binomial error structure within our GLMs. However, the reasons for the greater effectiveness of our negative binomial GLMs over the GLS models are not so clear cut. One possible explanation for this is that GLS tends to give more importance to mechanisms acting at a local scale (Diniz-Filho *et al.* 2003; Hawkins *et al.* 2007) at the expense of long distance clinal trends.

There were seasonal differences in habitat use by all four gull species, with higher levels of fit observed during the summer than during the winter. The most striking difference observed was the coastal distribution of summer breeding sites in comparison with the more widely dispersed nature of the winter roost sites. Nationally and internationally important breeding grounds of the lesser black-backed and herring gulls around Morecambe Bay, in the North West of the study region (Stroud *et al.* 2001), resulted in a spatial structure to the residuals for the models of the summer distribution of these species. In both seasons, low values of θ indicate a high degree of clustering amongst gull

populations. To put these results into context it is necessary to consider the ecology of the species concerned.

The aggregation of gull roosts is likely to be caused by interactions between genes (Rodway & Regehr 1999), the behaviour of conspecifics and parents (Oro & Pradel 2000; Wagner *et al.* 2000; Danchin *et al.* 2001; Prevot-Juillard *et al.* 1998) and the surrounding environment (Horton *et al.* 1983; Duhem *et al.* 2007). However, disentangling these relationships is difficult. Previous studies (Prevot-Juillard *et al.* 1998) have shown that young gulls have a tendency to return to their natal sites. The use of sub-optimal breeding sites by competitively superior individuals (Rodway & Regehr 1999) implies that this may be the result of a genetic component to habitat selection. In contrast, the habitat copying hypothesis (Wagner *et al.* 2000; Danchin *et al.* 2001) proposes that individuals base their habitat choices on those of successful conspecifics. Whilst this hypothesis has yet to be supported in gull species (Parejo *et al.* 2006), colony size has been shown to influence recruitment more than either food availability or reproductive success (Oro & Pradel 2000). This suggests gulls use information from conspecifics when selecting roost or breeding sites. However, with expanding populations, space in breeding sites or winter roosts can be at a premium. Consequently, individuals arriving late or those which are at a competitive disadvantage are then forced to seek out alternative sites in neighbouring areas, leading to an aggregation of satellite roosts, splitting from the original.

Seasonal variation in habitat preferences will be related to behavioural differences imposed by processes such as migration and breeding. Provisioning for young is a major limiting factor for gulls during the summer. To maximise chick growth, access to a reliable food source is required (Rodway & Regehr 1999; van Klinken 2002). However,

for healthy growth specific nutrients, found only in natural food sources, like fish, are required (Pierotti & Annett 1991). This is borne out by the coastal distribution of breeding colonies, their association with fishing ports and the presence of gulls at fisheries discards during the summer (Furness *et al.* 1992). Understanding the importance of the supplemental feeding provided by fisheries discards to seabirds has been identified as an ecological question of high policy relevance (Sutherland *et al.* 2006). This evidence shows that this resource can be highly important to breeding gulls.

During the winter, with no young to care for and the population swollen by migrants from Scandinavia and continental Europe (Wernham *et al.* 2002), it may be expected that the distribution of gulls is limited by food availability. However, whilst there were associations with human mediated landscapes, like urban and arable areas, only the black-headed gull showed an increase in roost size in response to proximity to landfill sites. Gulls are capable of travelling large distances on a daily basis in order to feed (Cramp *et al.* 1983; Karlsson 2003), and some, such as the herring gull, can be highly aggressive (Sibly & McCleery 1983). The black-headed gull may roost close to landfill sites, in order to exploit these food sources to their maximum before larger, more aggressive species arrive. In contrast to many other avian species, it appears that the availability of food limits the distribution of gulls more during the summer than the winter (Houston & McNamara 1993; Canterbury 2002; Moorcroft *et al.* 2002; Peach *et al.* 2003; Robb *et al.* 2008).

Overall, it was easier to explain the distribution of gulls during the summer, when their behaviour was constrained by provisioning for young, than during the winter. Consequently, it is easier to predict how gulls will disperse within the landscape during the summer, making their populations easier to manage at this time. Belant (1997) calls

for better spatial coordination in management to effectively manage the problem caused by urban gulls. However, the effects of migration and dispersal mean that it is not possible to know what the effect of controlling birds on one site during the winter will have on birds on their breeding grounds, and *vice versa*. Indeed, there are indications that the effects of meta-population dynamics can hamper attempts to control problem populations (Bosch *et al.* 2000). Therefore, in order to develop effective control strategies it is important to gain a better understanding of the movements between roosts and breeding colonies. This would enable not just a spatial coordination in management, but also a temporal coordination.

Chapter 4: Gull Strikes on RAF Aircraft: Towards the Creation of a UK Bird Avoidance Model

Abstract

Collisions between aircraft and birds cost the aviation industry a substantial sum every year and put human lives at risk. Between 1990 and 2005 there were over 3000 bird strikes on Royal Air Force (RAF) aircraft over mainland England and Wales, whilst many of the species involved were not identified, at least 404 were gull species (*Larus* spp.) which pose a particular hazard as a result of their large body size and tendency to flock. Gulls are a social family, often roosting in large groups. We used bivariate k means clustering to determine whether the distribution of gull-aircraft collisions was dependent on the distribution of large gull roosts. Gull strikes were significantly clustered around gull roosts with over 1000 individuals and landfill sites at distances of around 6 000 metres. There was weak evidence for the clustering of strikes around RAF airfields at low altitudes. Strikes involving unknown species showed a similar distribution, suggesting that many of these may also have involved gull species. This information can be used to reduce the risk of collisions between RAF aircraft and gulls both through the landfill planning process and as the basis of a United Kingdom Bird Avoidance Model. This methodology can be applied to other species and families involved in bird strikes to create a more detailed map of the United Kingdoms bird strike risk.

Introduction

Damage to aircraft as a result of collisions with avian species causes substantial losses to the aviation industry as a result of the resulting repairs and delays (Richardson & West

2000; Allan & Orosz 2001; Allan 2002; Sodhi 2002; Thorpe 2003). The probability of a costly bird strike both in terms of loss of life, and financial impact is thought to be increasing (Robinson 2000). Between 1950 and 1999 birds were involved in 286 collisions with military aircraft worldwide that resulted in either the death of aircrew or the destruction of aircraft (Richardson & West 2000), with numbers rising during the 1990's. Whilst the majority of bird strikes have a far less severe outcome, in the United Kingdom they still cost the Royal Air Force (RAF) in the region of £12 million annually (Allan 2002). Whilst bird strikes have attracted a great deal of attention in the "grey" literature (i.e. Richardson 1994; Bell 1999, Cleary *et al.* 2006), few authors have addressed the topic in the scientific press (i.e. Lovell & Dolbeer 1999; Dolbeer 2006).

Whilst civilian light aircraft are affected by bird strike (i.e. Thorpe 2003), the nature of military training exercises leaves them particularly vulnerable to bird strikes, and at a greater risk of damage as a result. As most bird strikes occur at altitudes of less than 500 feet (Dolbeer 2006), civilian light aircraft tend to be vulnerable only during take off and landing (Sodhi 2002). A number of strategies have been developed to deal with the problem of large numbers of birds of congregating around airfields including habitat management, such as reducing the quantity of standing water (Gabrey & Dolbeer 1996; Blackwell *et al.* 2008) or increasing the length of grass (Brough & Bridgmen 1980), and bird harassment regimes involving dogs (Froneman & van Rooyen 2003), birds of prey (Erickson *et al.* 1990) and shooting (Dolbeer *et al.* 1993). However, the lower altitudes and high speeds used by military pilots means that they are also vulnerable to collision with birds whilst they are en route between airfields or on manoeuvres (Sodhi 2002). The high speeds reached by military aircraft during their manoeuvres means that any damage sustained as a result of a bird strike is likely to be greater than that sustained on or around an airfield (Dekker *et al.* 2006).

As a result, there is a need to develop measures to reduce the risk of collisions between birds and aircraft occurring away from airfields. A number of countries have used historical data describing the distribution of bird strikes and variation in species abundance (Lovell & Dolbeer 1999; Dekker & van Gasteren 2005) to identify areas in which there is a particularly high risk of bird strike and create Bird Avoidance Models (BAMs). To create an effective BAM it is necessary to understand the factors responsible for spatial variation in bird strike risk.

The species or families of birds involved in collisions with aircraft often remain unidentified, however, of those that are identified, gulls usually constitute the majority (Dolbeer *et al.* 2000; Dekker *et al.* 2006). Whilst other families, such as hirundines and columbids, also feature heavily in bird strike reports (Dekker *et al.* 2006), gulls are of a particular concern due to the high probability of damage being caused during a collision with an aircraft as a result of their large body size (Dolbeer *et al.* 2000) and tendency to flock (Carter 2001). The congregation of gulls in large numbers at their roost sites or, when feeding in areas like landfill sites, may pose a particular risk to aircraft. We investigate the strikes on RAF aircraft in England and Wales by gull species (*Larus* spp.) between 1990 and 2006, in order to determine whether these strikes were clustered around roost sites, landfill sites and RAF airfields. We then investigate the effects of altitude on the clustering of gull strikes. This information is used as the basis for a BAM for England and Wales. Finally, the habitat features of key sites are investigated in order to identify sites which may pose a risk to aircraft in the future.

Methodology

Between 1990 and 2006 there were over 3 000 collisions between birds and Royal Air Force (RAF) aircraft in the British Isles. Of these, we limited our analysis to those

occurring over England and Wales due to the limitations imposed by the data regarding gull roosts and landfill sites. This left 404 strikes which were known to have involved gull species (*Larus* spp.). Data on gull roost sites were obtained from the British Trust for Ornithology's (BTO's) 2003 Winter Gull Roost Survey (WinGS), landfill site locations were obtained from the Environment Agency REGIS database and RAF airfield locations were obtained from the RAF (Pandora data base).

Clustering of strikes on RAF aircraft by gull species

Bivariate k-means clustering was used to investigate the distribution of gull strikes in relation to gull roost sites, RAF airfields and landfill sites accepting domestic refuse. Bivariate k-means clustering is used to characterize the spatial relationship between two sets of points within a given area (Rowlinson and Diggle 1993). This is done by assessing the number of cases (in this case, gull strikes) within a given radius of an arbitrary control (in this case, gull roosts, landfill sites or RAF airfields) (Fig. 4.1.). For both controls and cases a k-function is calculated to determine the degree of clustering. The k-function is defined as the number of events within a given distance of an arbitrary event, divided by the overall intensity of events. Where significant clustering occurs, more pairs of points are separated by a given distance than would be expected in a random pattern. The degree of clustering is determined by calculating the difference between the k-functions for the controls and cases. Under the null

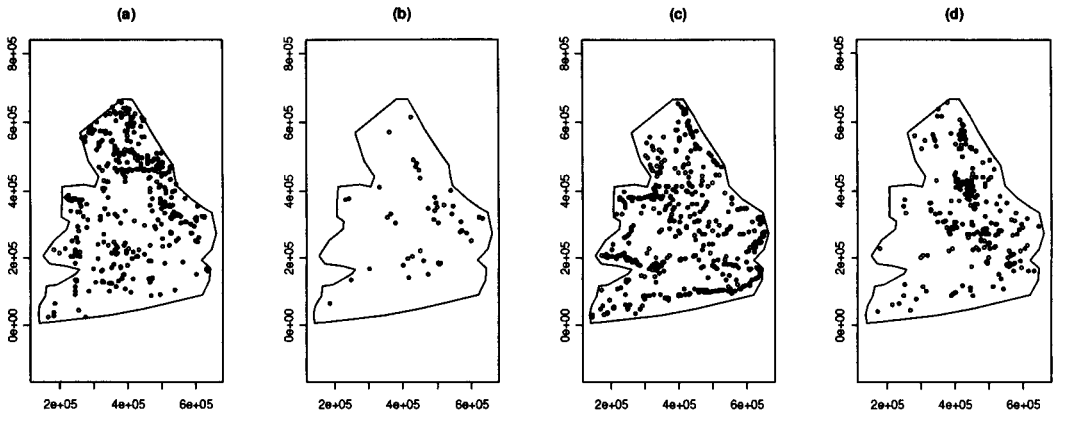


Figure 4.1. The distribution of gull strikes (a), RAF airfields (b), gull roosts (c) and landfill sites (d) throughout England and Wales

hypothesis of complete spatial randomness, this difference will be zero. To assess whether the cases are spatially dependent on the controls a two standard deviation envelope (representing 95% confidence intervals) is calculated using the difference between k-functions. Spatial dependence occurs where the difference between k-functions is more than 2 standard deviations different from zero. A difference of more than zero represents clustering, whilst a difference of less than zero represents repellence. This can be assessed graphically within the R extension Splancs (Rowlinson & Diggle 1993).

We analysed the extent of clustering of strikes around roosts of 6 different size classes (all roosts, >100 individuals, >500 individuals, >1000 individuals, >5000 individuals and >10000 individuals) to identify an optimal size at which gull roosts became a problem. The risk posed by each roost is likely to be related to its size, with smaller roosts posing less of a problem. Therefore, by excluding roosts that fall below a minimum size threshold it will be possible to develop a more realistic bird avoidance model. Having investigated the clustering of gull strikes at all altitudes around the roosts, landfills and RAF stations, we then split the data into 3 height

classes (<100 feet (n=119), 100-250 feet (n=146) and >250 feet (n= 139)). Finally, we used 402 records of strikes from the same period and area involving unidentified species, to determine the possible involvement of gulls in these strikes. This information then formed the basis of a bird avoidance model.

Key features of roost sites

Having identified an optimal size at which gull roosts posed a threat to RAF aircraft, we investigated key habitat features of these roosts. All sites above this size were divided into those which were inland roosts and those that were coastal roosts.

Whilst we knew where roost sites occurred, it was also necessary to consider where they did not occur, consequently we used a Monte-Carlo approach similar to that of Rushton *et al.* (2006), comparing the distribution of known roost sites to the distribution of a series of randomly sampled points. Ten thousand points on both the coast and inland water bodies were randomly selected using the GRASS 6.2 GIS package. These were then combined into two datasets with their respective set of roost sites. For each dataset we identified the land use of the surrounding 1 km^2 using the UK 25m land cover map, altitude and distance to nearest landfill site. The land use data for each set of sites was then summarised using Detrended Correspondence Analysis (DCA) within the R extension vegan (Oksanen *et al.* 2007). For inland sites, water body surface area was also calculated.

To identify the key features of each set of roost sites, they were compared to an equal number of randomly sampled sites and a full model was fitted using a binomial Generalized Linear Model (GLM). Relative to the total area available, the number of gull roost sites was low, consequently the analyses were repeated 1000 times using

1000 different selections from our randomly sampled points to assess the robustness of the models. This is effectively a compromise between maximising the efficiency of the logistic regression analyses and covering the range of variation in explanatory variables in areas in which gull roosts were not recorded. Model significance was assessed on the basis of how many times out of the 1000 runs the regression coefficient for each explanatory variable was significant. The models were then simplified by dropping non-significant variables and assessing changes in the mean Aikaike's Information Criterion (AIC) for each replicate, until the most parsimonious model remained.

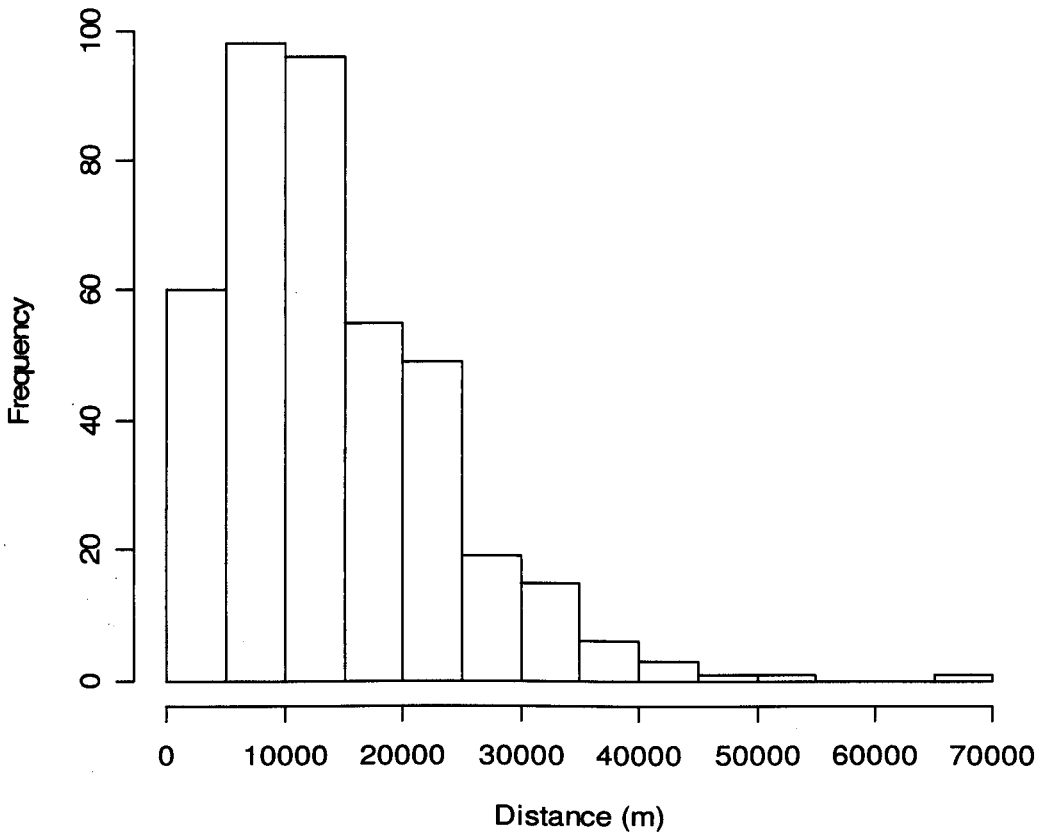


Figure 2 Frequency distribution of distance from gull strikes to gull roosts, (1st quartile 7040 m, median 12 200 m, mean 14 050 m, 3rd quartile 19 410 m)

Results

Clustering of strikes on RAF aircraft by gull species

Gull strikes on RAF aircraft over mainland England and Wales occurred an average of 14 km from gull roost sites (Fig. 2.). There was significant clustering of gull strikes within 7.5 km of landfill sites, but not around RAF airfields (Fig. 3). Significant clustering of strikes was detected around roost sites of all sizes at distances of up to 6

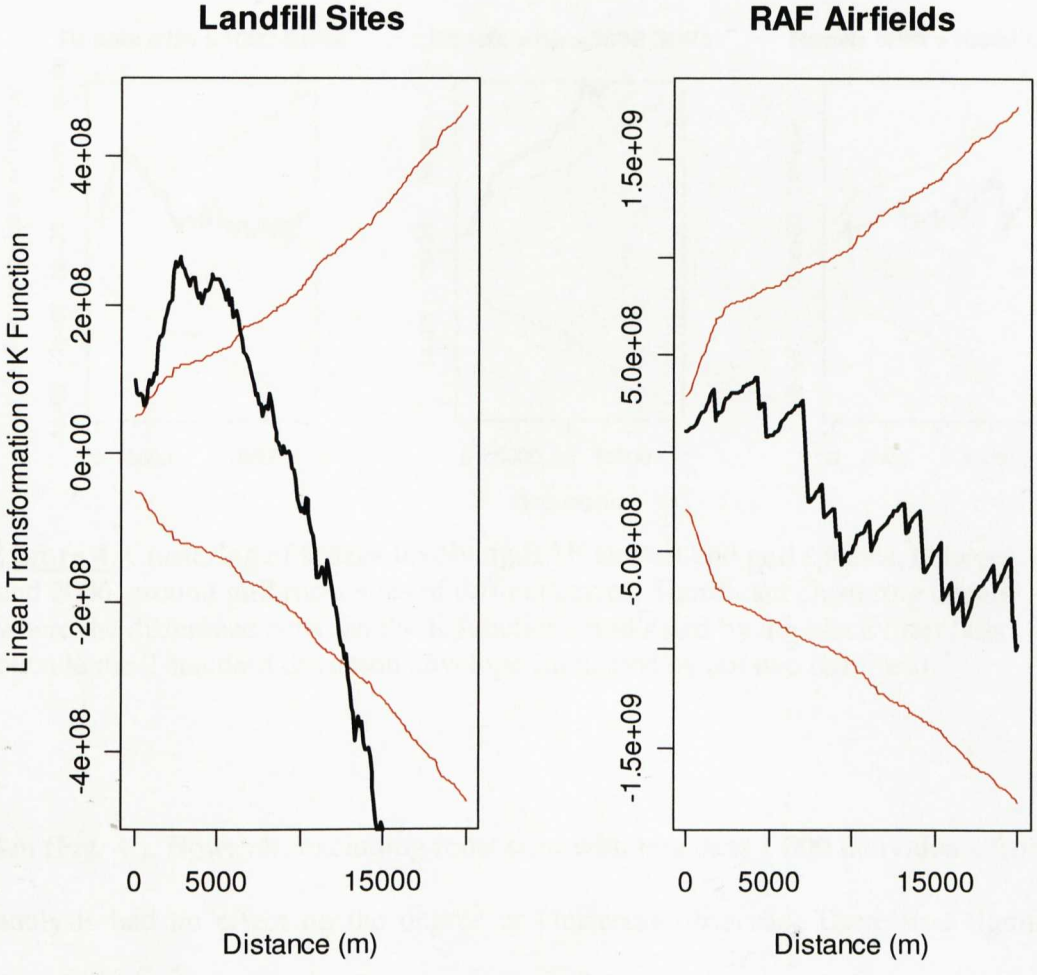


Figure 3 Clustering of strikes involving RAF aircraft and gull species, between 1990 and 2006, around RAF airfields and Landfill sites. Significant clustering occurs where the difference between the K functions (indicated by the black line) falls outside the 2 standard deviation envelope (indicated by the two red lines).

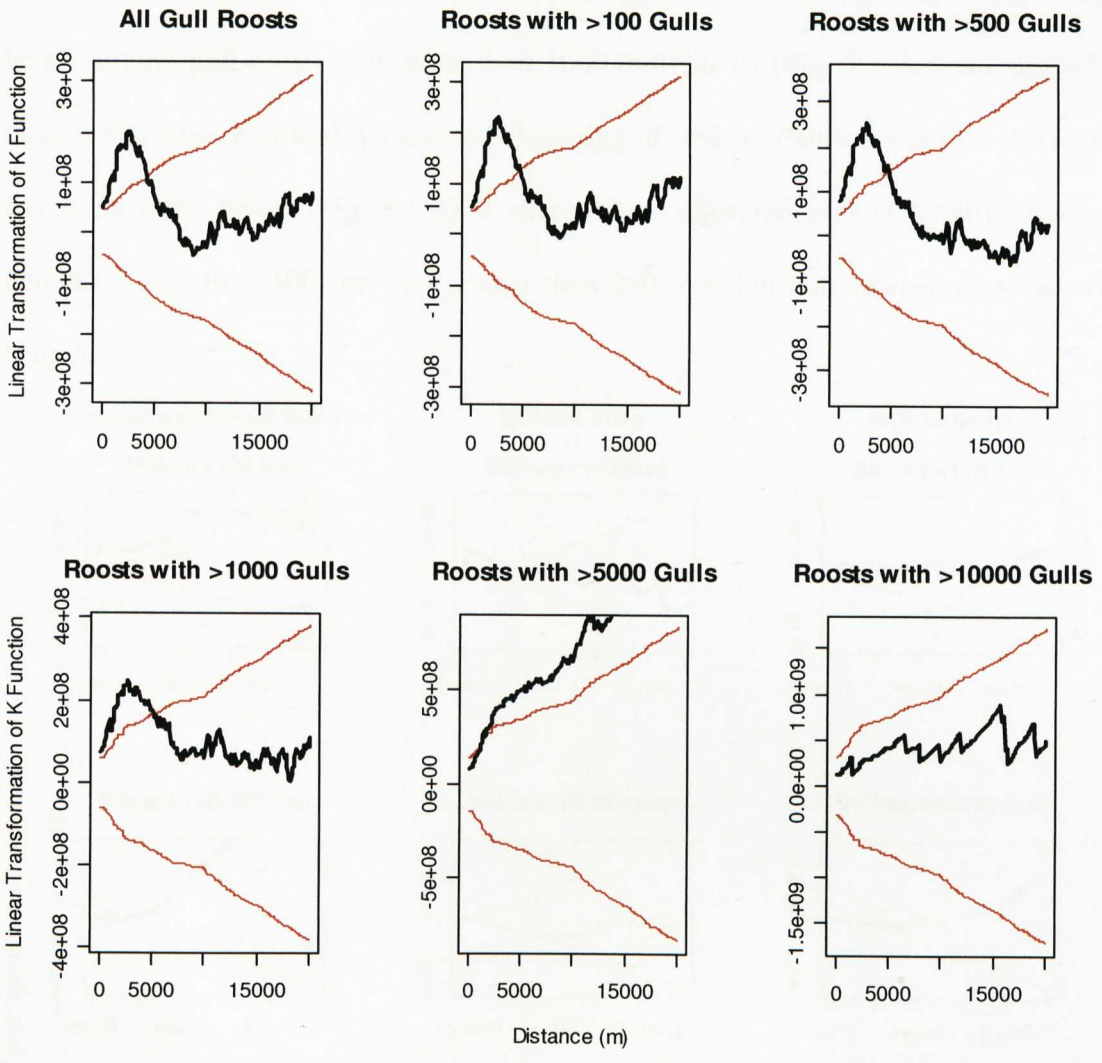


Figure 4 Clustering of strikes involving RAF aircraft and gull species, between 1990 and 2006, around gull roost sites of different sizes. Significant clustering occurs where the difference between the K functions (indicated by the black line) falls outside the 2 standard deviation envelope (indicated by the two red lines).

km (Fig. 4.). However, excluding roost sites with less than 1 000 individuals from the analysis had no effect on the degree of clustering observed. There was significant clustering of strikes at distances of more than 5 km at roost sites with more than 5 000 individuals, but there was no evidence of significant clustering around roost sites with more than 10 000 individuals (Fig. 4.). Consequently, further analysis was limited to those roost sites which had more than 1000 individuals.

When the altitude of strikes was considered, significant clustering was found at all levels around gull roosts with more than 1000 individuals (Fig. 5.). Around airfields there was evidence of highly localised clustering of strikes at altitudes below 100 feet, but at no other levels (Fig. 5.). Gull strikes were clustered around landfill sites at heights of less than 100 feet and greater than 250 feet, but not between these levels (Fig. 5.).

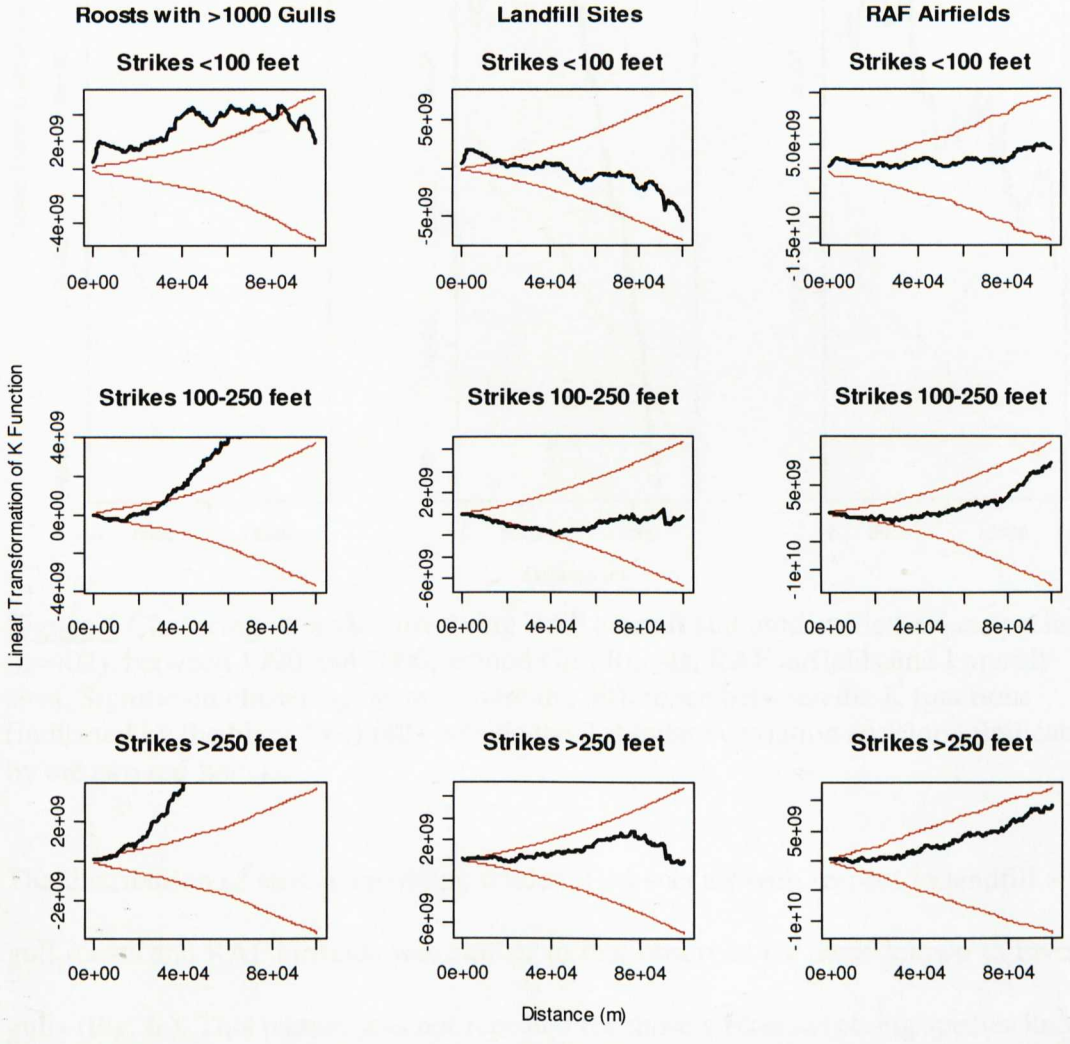


Figure 5 Clustering of strikes involving RAF aircraft and gull species, between 1990 and 2006, around roosts with >1000 individuals, RAF airfields and Landfill sites at different height bands. Significant clustering occurs where the difference between the K functions (indicated by the black line) falls outside the 2 standard deviation envelope (indicated by the two red lines).

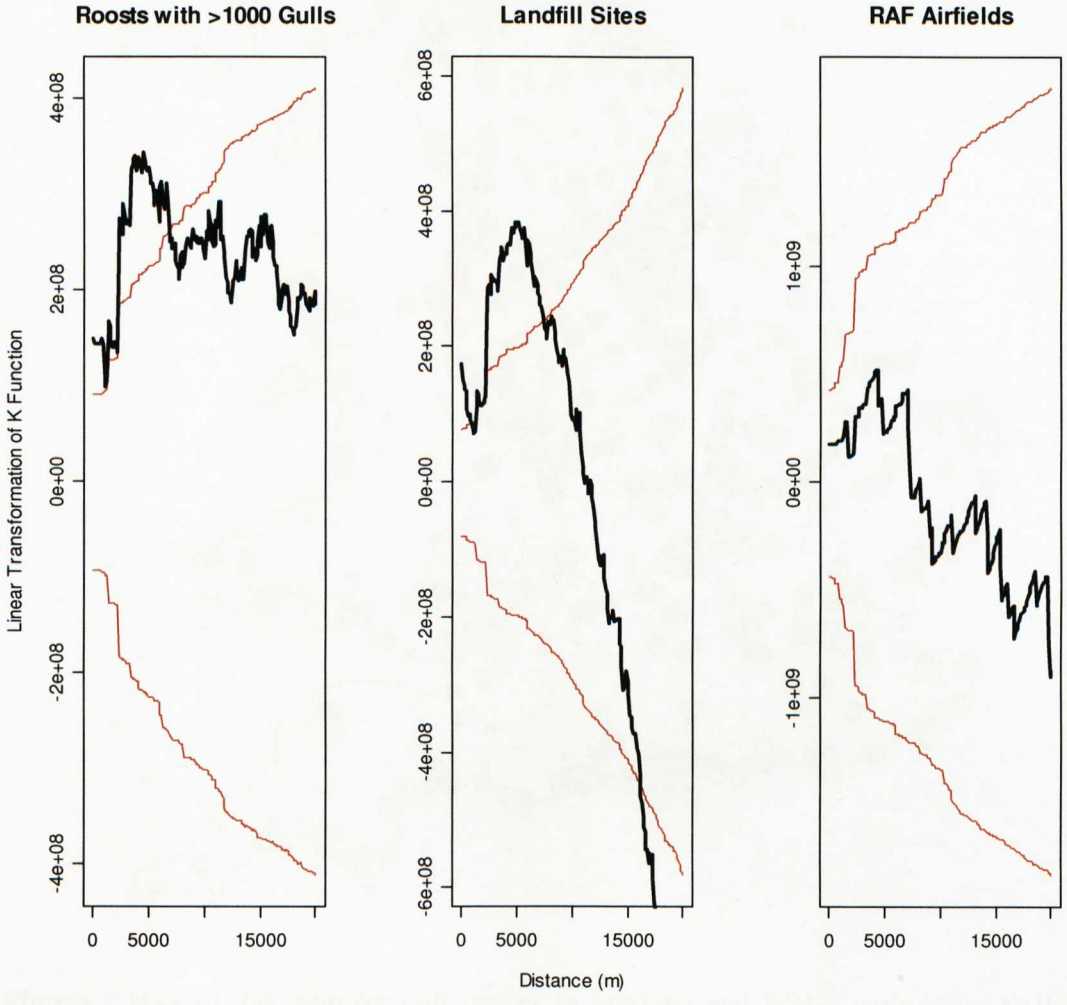


Figure 6 Clustering of strikes involving RAF aircraft and unidentified avian species (n=402), between 1990 and 2006, around Gull Roosts, RAF airfields and Landfill sites. Significant clustering occurs where the difference between the K functions (indicated by the black line) falls outside the 2 standard deviation envelope (indicated by the two red lines).

The distribution of strikes involving unidentified species with respect to landfill sites, gull roosts and RAF airfields was similar to that observed for those known to involve gulls (Fig. 6.). This pattern was not repeated for those strikes involving species known not to be gulls.

This information can be used as the basis for a BAM. The bivariate k-function analysis shows that strikes are significantly clustered in the 6 km surrounding roosts with more 1000 gulls and in the 7.5 km surrounding landfill sites. Using these values

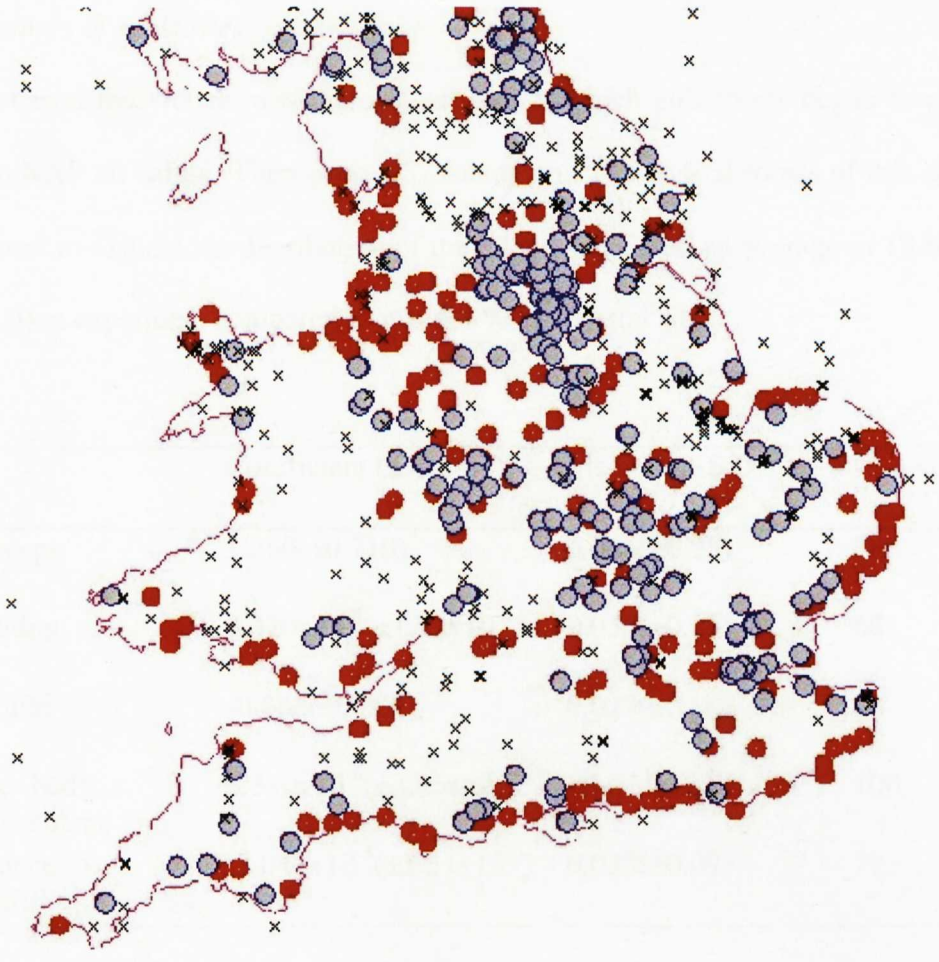


Figure 7 Hazard risk map for gull strikes in England and Wales with major (>1000) gull roosts (red circles), landfill sites (blue circles) and the location of known gull strikes (x's) shown

to buffer the roosts and landfill sites, a risk map can be created (Fig. 7.). This highlights a number of areas with a high density of roosts and landfill sites that pose a particularly high risk of gull strike. A comparison with the actual distribution of strikes shows that this risk map is reasonably accurate. Unfortunately, data on flight paths were not available for comparison.

Key features of roost sites

One thousand individuals was the optimal size at which gull roosts began to pose a threat to RAF air safety. There were 132 inland and 146 coastal roosts of this size. It was easiest to explain the distribution of the inland sites, with an average of 19.8 % of the variation explained, compared to just 6.8 % for coastal sites.

	Coefficient (± S.D.)	Mean P (± S.D.)	% P <0.05
Intercept	1.260(±0.710)	0.048(±0.25)	78
Northing	$3.320 \times 10^{-6}(\pm 1.52 \times 10^{-6})$	0.055(±0.28)	68
Altitude	-0.006(±0.002)	0.029(±0.16)	83
Water body Surface Area	$8.340 \times 10^{-6}(\pm 3.96 \times 10^{-6})$	$<0.001(\pm 2.81 \times 10^{-5})$	100
Distance to Landfill	$-8.047 \times 10^{-5}(\pm 2.31 \times 10^{-5})$	0.033(±0.09)	79

Table 1. Most parsimonious GLM predicting the presence of inland gull roosts with >1000 individuals (AIC 234.21 ± 33.94 S.D.), $d^2 = 0.198$ (±0.03 S.D.)

For inland roost sites, the most important predictor was water body surface area, which was identified as being significant in all 1000 models (Table 1.). Water bodies on which gulls roosted had an average surface area of 716 000 m², compared to just 65 000 m² for those gulls were absent from. Northing, altitude and distance to landfill site were also identified as factors likely to influence the distribution of inland gull roosts, and were significant in 68%, 83% and 79% of models respectively. The mean regression coefficients indicate that there was a tendency for gull roosts to have a southerly distribution, and to occur at low altitudes (Table 1.). There was also a tendency for roosts to occur in close proximity to landfill sites in comparison with our randomly selected sites.

For coastal sites, Easting, altitude and the third and fourth axes of the DCA of land cover were identified as important factors in explaining the distribution of gull roosts,

	Coefficient (± S.D.)	Mean P (± S.D.)	% P <0.05
Intercept	-2.15(±0.29)	<0.0001(±0.0001)	100
Easting	$4.56x10^{-6}(\pm 7.38x10^{-7})$	<0.0001(±0.0001)	100
Altitude	0.07(±0.04)	0.0200(±0.0100)	98
DCA Axis 3	-1.59(±0.24)	<0.0001(±0.0004)	100
DCA Axis 4	1.50(±0.32)	0.0100(±0.0200)	95

Table 2. Most parsimonious GLM predicting the presence of coastal gull roosts with >1000 individuals (AIC 370.05 ± 11.08 S.D.), d^2=0.068 (±0.013 S.D.)

significant in 100%, 98%, 100% and 95% of models respectively. The mean regression coefficients (Table 2.) indicate that the roosts have an easterly distribution, with slightly elevated positions. The third DCA axis represents a trend of decreasing urbanisation, whilst the fourth axis represents a trend from inland water to estuarine systems (Fig. 8.). The regression coefficients for the third and fourth axes indicate that gull roosts are associated with urbanised areas, with access to estuarine habitats. However, the low values of variation explained for coastal roosts distribution, shows that it will be hard to predict the distribution of gulls around the coast.

Discussion

Collisions between gulls and military aircraft were not randomly distributed with respect to either landfill sites or gull roosts. Clustering was significant at all altitudes

around roost sites, and at altitudes of less than 100 feet and more than 250 feet around landfill sites. Around RAF airfields, there was evidence of highly localised clustering occurring only at low altitudes, indicating the likely involvement of aircraft taking off

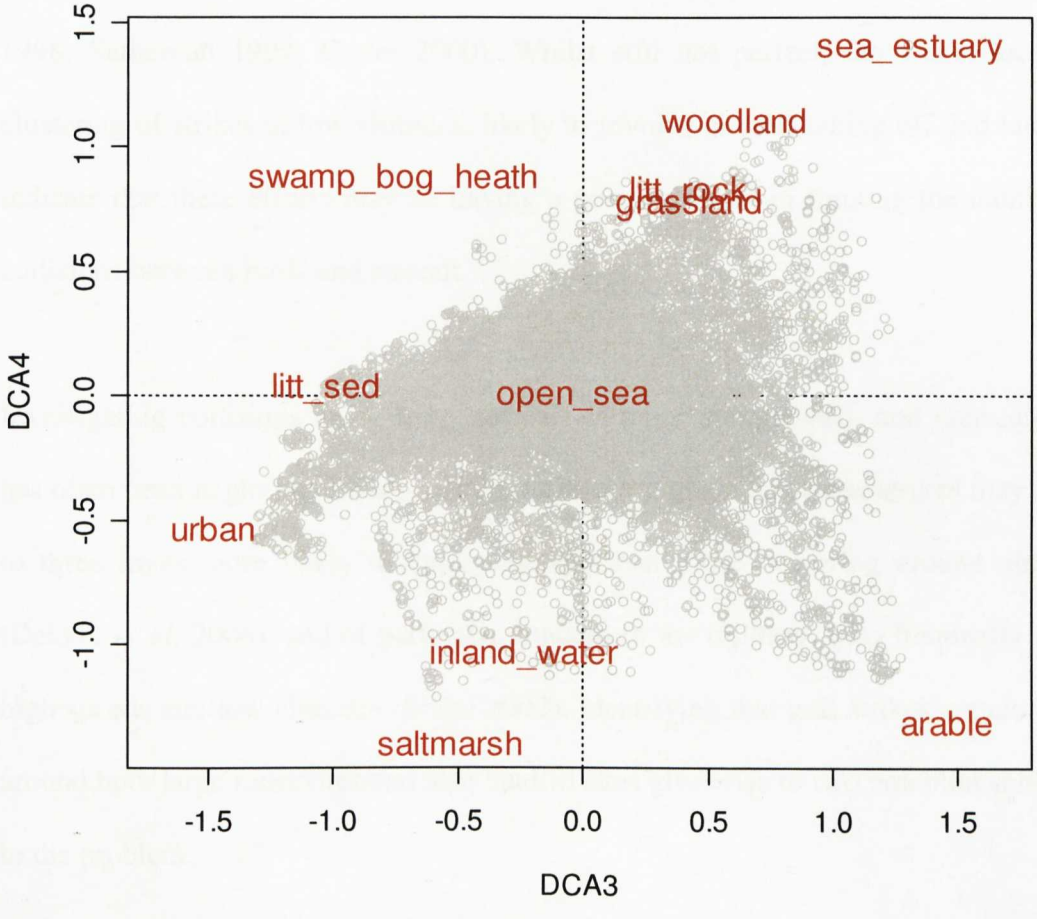


Figure 7. 3rd and 4th axis of Detrended Correspondence Analysis (DCA) of habitat based on CEH landcover data for coastal gull roosts and random points in England and Wales. The third axis represents a trend from urban to arable environments whilst the fourth axis represents a trend from freshwater to estuarine habitats.

or landing. This allows us to identify areas, like large water bodies close to landfill sites, likely to represent a threat to RAF aircraft as a result of the presence of large numbers of birds.

On and around airfields, gulls are heavily involved in collisions with aircraft. However, the patterns of strikes around airfields have been widely studied and are in general well understood (i.e. Linnell *et al.* 1996). As a result, there are a wide variety of measures available to reduce the numbers of problem species on and around airfields, and therefore, the bird strike risk (Montoney & Boggs 1993; Ballinger *et al.* 1998; Satheesan 1999; Carter 2000). Whilst still not perfect, the weak, localised clustering of strikes at low altitudes, likely to involve aircraft taking off and landing, indicate that these efforts may be having a positive effect in limiting the number of collisions between birds and aircraft.

Investigating collisions away from airfields is more complicated, and consequently has often been neglected. This is of serious concern given that these strikes may be up to three times more likely to cause damage than those occurring around airfields (Dekker *et al.* 2006), and of particular concern to the military, who frequently fly at high speeds and low altitudes (Sodhi 2002). Identifying that gull strikes are clustered around both large roost sites and also landfill sites gives rise to two potential solutions to the problem.

The traditional approach to managing the risk of bird strikes away from airfields is the development of bird avoidance models (Lovell & Dolbeer 1999; Dekker & van Gasteren 2005). However, these often operate at too coarse a scale to be of practical use (Dekker & van Gasteren 2005). Using bivariate k-function analysis it was possible not only to identify that large aggregations of birds posed a risk to aircraft, but at what scale this risk exists. This allows the creation of a BAM at a more realistic scale, by setting up aircraft exclusion zones surrounding major gull roosts and landfill sites.

These models can be further refined. The flight patterns of birds vary seasonally and hourly and can be influenced by local weather conditions (Manteklow 2000; Shamoun-Baranes *et al.* 2006). By building these factors into any BAM it will be possible to accurately forecast the risk of gull strike at any given point, at any given time.

The identification of large roosts and landfill sites as hazardous to military aircraft on manoeuvres also allows a more proactive approach to be taken to reduce bird strike risk. Making landfill sites less attractive to birds through improved bird harassment regimes and altering tipping behaviour (Burger 2001; Cook *et al.* 2008; Soldatini *et al. 2008*) will reduce the number of gulls that gather to feed. This in turn will reduce the risk of gull strike. In addition, European plans to reduce the amount of waste sent to landfill sites (European Union Landfill Directive 1999/31/EC) means that many are being decommissioned. By working with aviation authorities it will be possible to directly target landfill sites on heavily used flight paths for decommissioning.

Large roosts within heavily used flight paths can also targeted. Bird harassment regimes are unlikely to be effective in this instance as they only work where alternative roosts are available nearby (Gosler *et al.* 1995). Consequently, a more drastic solution is necessary. Previously, to prevent bird strikes around airports, gulls have been culled (Dolbeer *et al.* 1993). By focussing on large roosts, in areas where gull populations are particularly hazardous, this could be an effective way to reduce the bird strike risk.

A consistent problem with the investigation of bird strike occurrence is that they are consistently under reported, and the species concerned often remains unidentified (Chilvers *et al.* 1997; Linnell *et al.* 1999; Barras & Dolbeer 2000). Arguably, if the reporting rate and species identification are correlated with species size, as suggested by some authors (i.e. Linnell *et al.* 1999), this may not be a serious issue as smaller birds are less likely to cause damage than large birds. However, Barras & Dolbeer (2000) found that the likelihood of a strike being reported was independent of species size. Our results would appear to support this hypothesis, with strikes involving unidentified species closely matching the distribution of strikes involving gulls. In contrast to the previous studies which were carried out around airfields, it was not possible to collect all of the carcasses of birds involved in bird strikes as part of our study, as the strikes occurred over a much larger area. However, a number of techniques are being developed that could allow the identification of unknown species. Chief amongst these is the analysis of blood or other tissue through DNA bar-coding (Herbert *et al.* 2004; Dove *et al.* 2006; Dove *et al.* 2008). Other techniques include the analysis of feather samples (Dove 1999) and the search for a "bird strike syndrome" (Lyne *et al.* 1998; Sheehy *et al.* 2003), whereby submitted birds can be examined for injuries consistent with aircraft collisions.

As a result of this study it has been possible to develop a basic BAM for gulls in England and Wales. This methodology can be easily applied to other avian species. The incorporation of bird movement data, climatic information and crucially a better knowledge of the species involved in bird strikes will allow the development of a truly effective and flexible BAM. By combining this BAM with targeted habitat

management, there is the potential to dramatically reduce the incidence of bird strike in the United Kingdom.

Chapter 5: Salmonella incidence amongst wild birds in England and Wales between 2003 and 2006

Abstract

Salmonella is a major zoonotic pathogen, and cases in both humans and livestock have been linked to outbreaks in wild birds. Attempts to quantify patterns in salmonella incidence amongst wild bird species have been unsuccessful because limitations imposed by sampling often lead to relatively small sample sizes. We use a combination of survival analysis and Canonical Correspondence Analysis (CCA) to investigate trends in wild bird salmonella prevalence. Using these techniques, it was possible to identify significant seasonal and spatial patterns in salmonella incidence amongst wild bird species. Salmonella in wild birds is associated with cattle farming and there are peaks in prevalence during the winter and spring. Passerine species are more susceptible to salmonella infection than non-passerine. We discuss the implications these results have for the potential zoonotic transmission of salmonella.

Introduction

In the United Kingdom each case of salmonella costs the economy an average of £606 once treatment and lost working time are accounted for. With 519 669 cases between 1981 and 2006 (H.P.A. 2008), this represents a substantial financial drain.. A number of studies have linked cases of salmonella in humans to those in wild birds (Kapperud *et al.* 1998; Tauni & Osterlund 2000; Alley *et al.* 2002; Nesse *et al.* 2005; Palmgren *et al.* 2005). The isolation of antibiotic resistant strains of salmonella from wild birds (Literak *et al.* 2007) makes this association particularly concerning.

A number of pathways have been proposed for the transmission of salmonella from wild birds to humans. One potential route involves the infection of livestock, such as cattle, which come into contact with salmonella infected bird faeces both in the general environment (Pangoli *et al.* 2008) and through contaminated food stuff (Daniels *et al.* 2003). Gulls have been proposed as a possible vehicle for the cross contamination of fish meal factories with salmonella (Nesse *et al.* 2005). Outbreaks of salmonella in cats, both in the UK and in Sweden, have been linked to the predation of wild birds (Tauni & Osterlund 2000; Philbey *et al.* 2008). Given that a wide range of species including, garden birds (Wilson & MacDonald 1967; Pennycott *et al.* 2002; Refsum *et al* 2003; Pennycott *et al.* 2005), gulls (MacDonald & Brown 1974; Palmgren *et al.* 2006) and raptors (Millan *et al.* 2004; Palmgren *et al.* 2004; Blanco *et al.* 2006), have been found to carry salmonella, the importance of these different pathways and therefore risk of zoonotic infection, is likely to vary with the ecology of the species concerned.

Whilst a number of studies have identified the potential hazard posed by salmonella infected wild birds (i. e. Refsum *et al.* 2002; Refsum *et al.* 2003; Pennycott *et al.* 2006), few have attempted to quantify patterns of infection in birds statistically. One probable reason for this is that whilst many studies initially appear to have large sample sizes, often several hundred individuals (i.e Refsum *et al.* 2002), limitations imposed by sampling methodologies mean that when species composition and distribution are considered, these are often deceptive. This means that assessing the magnitude of salmonella carriage in birds and its relative significance is difficult.

We use Canonical Correspondence Analysis (CCA) and survival analysis to investigate spatial and temporal trends in salmonella occurrence amongst wild birds. Multivariate techniques, such as CCA, allow us to summarise patterns in species distribution across regions. Furthermore, canonical approaches, like CCA, can be used to investigate the role of covariates in determining the major trends in the data (Oksanen *et al.* 2007). This allows us to relate the species residing in any region to local habitat and epidemiological factors that might predispose them to salmonella carriage. These techniques are used extensively in ecological research to investigate factors determining animal and plant community structure, but with far less frequency in epidemiological studies where the focus is usually on cases of a single pathogen amongst the population of an individual species.

The detection of a salmonella infected bird at a laboratory can be considered an "event". By understanding the factors that impact on the "event" it may be possible to identify factors leading to it, and to identify differences across the system where the event has occurred. Survival analysis concerns the investigation of the distribution of a series of events over a given time period (Venables & Ripley 2002). Whilst survival analysis has traditionally been used to investigate factors such as investigating organisms survival (i.e. Samo *et al.* 1999; Johnson *et al.* 2004) or the effects of toxins (i.e. Roy & Campbell 1995; Lepeule *et al.* 2006), recently studies have employed it in novel ways. Boqvist and Vogsholm (2005) use survival analysis to investigate factors related to Swedish cattle farms being released from salmonella related restrictions. We employ a similar methodology to investigate factors related to salmonella prevalence in wild birds using Cox proportional hazard models with an Anderson-Gill counting process. Cox proportional hazard models assume that there is an underlying

baseline hazard remaining constant through time, while the Anderson-Gill counting process allows the incorporation of multiple, ordered and independent events (Therneau 2008). Using this methodology, it is not necessary to examine absolute numbers of infected individuals, only to know whether or not an infected individual has been found in any given area at any given time.

A better understanding of the epidemiology of diseases in wildlife reservoirs has been identified as a key ecological question of high policy relevance in the UK (Sutherland *et al.* 2006). We use survival analysis and CCA to investigate how human land use, and in particular agriculture, influences salmonella infection in wild birds. We then determine what seasonal trends exist in wild bird *Salmonella* prevalence, and relate this to the biology of the species concerned.

Methodology

Between 2003 and 2006 6 489 dead birds were submitted to the Veterinary Laboratories Agency (VLA) through 14 regional laboratories in England and Wales as part of the Diseases of Wildlife scheme. It was not always possible to identify these individuals to species level, so in order to maximise the sample size they were split into approximate family groups (Table 6.1.). These samples were tested for the presence of *Salmonella* serotypes, and the distribution of *Salmonella* infected individuals was then analysed using CCA and Survival Analysis.

Species Group	Number Sampled	Number Positive
Auk	207	7
Bird Of Prey	183	1
Bunting	6	
Corvid	519	1
Diver	3	
Duck	1571	30
Dunnock	9	2
Finch	710	239
Flycatcher	1	
Fulmar	5	
Goose	500	1
Grebe	5	
Grouse	6	
Gull	265	50
Heron	17	1
Hirundine	34	
Kingfisher	4	2
Nuthatch	3	
Partridge	7	1
Phalacrocoridae	25	
Pheasant	30	
Pigeon	646	20
Pipit	1	
Rail	58	6
Shearwater	27	
Sparrow	134	46
Starling	268	1
Swan	930	15
Swift	12	
Tern	11	
Thrush	205	1
Tit	32	
Wader	10	
Wagtail	32	
Warbler	2	
Waxwing	1	
Woodpecker	9	
Wren	1	
TOTAL	6 489	424

Table 6.1 Total individuals received and testing positive by family or order.

Collation of Covariates

In order to investigate what factors affected the spatial distribution of our samples, they were grouped according to the regional laboratory receiving them. A catchment area for each regional laboratory was then defined using Thiessen polygons in

GRASS 6.2 (GRASS development team 2008). These were then used to extract information on land use (CEH 2000), weather (Hijmans *et al.* 2005) and livestock (DEFRA 2007). Weather was considered as an explanatory variable as *Salmonella* is likely to persist in the soil longer in regions where the climate is most favourable (i.e. Platz 1980; Davies & Breslin 2003). Certain land uses are more likely to result in *Salmonella* persistence in the soil, in particular farming, especially livestock production, it was hypothesised that *Salmonella* prevalence in wild birds would be highest in regions with a high concentration of livestock.

Canonical Correspondence Analysis

The carriage of salmonella by wild birds varied with species and region. We created matrices detailing the number of each family group received, and the proportion of each group with a salmonella infection by lab, and used CCA to investigate spatial patterns of salmonella infection. Due to the variation and biases associated with the sampling regime, only family groups which had tested positive for *Salmonella* in two or more laboratories and had been sampled on at least 100 occasions were analysed using CCA within the R extension vegan (Oksanen *et al.* 2007). Initially the distribution of samples received by each laboratory were analysed in order to investigate factors associated with regional differences in sampling.

When investigating how land use affected the spatial variation in salmonella prevalence, it was necessary to take into consideration the distribution of the original samples. By using a partial CCA, it was possible to investigate the spatial variation in salmonella prevalence while also excluding the effects of the original sampling regime. The effects of rainfall, temperature, habitat, geographic location and livestock

were considered as constraining variables for both ordinations and parsimonious models were selected by comparing Aikaike Information Criterion (AIC) (Oksanen *et al.* 2008).

Survival Analysis

The dead birds arrived in the laboratories on an ad hoc basis, where they were routinely tested for salmonella. The occurrence of an infected wild bird could be considered an "event", or a series of repeated events. Cox-proportional hazard models were used to investigate the extent to which the receipt of *Salmonella* infected birds could be explained by our covariates. These models assume that there is an underlying unspecified baseline hazard, which stays constant through time, that is influenced by covariates which enhance or mitigate the risk of an event occurring. Using both forward and backwards step-wise reduction a parsimonious model was identified from a full model with all covariates. Assumptions of proportionality were tested by plotting and visually assessing the time dependent coefficients for each covariate against time, and formally using a zph test which correlates the scaled Schoenfeld residuals with time for each covariate, and assesses significance with a two-sided χ^2 test. The data were then split into passerine and non-passerine families and this process was repeated for each seperately. All models were fitted using the survival extension in R (Therneau 2008).

Results

A total of 424 individuals (6.5%) were found to have tested positive for salmonella serotypes (Table 6.1.). Of these, *Salmonella* was most commonly recovered from finch species, which accounted for over half of the individuals testing positive, however, gulls, sparrows and ducks also contributed sizeable numbers to overall figures. Prevalence of *Salmonella* also varied both by lab and by season. A particularly high percentage of individuals submitted to the Truro laboratory (34%)

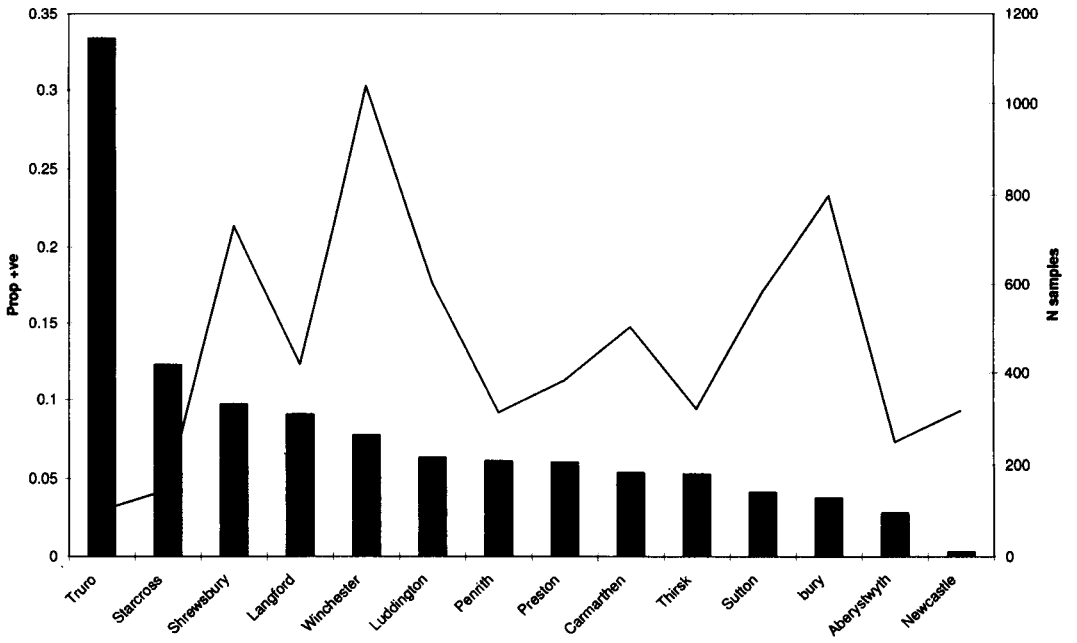


Figure 6.1 Variation in sample size (bars) and proportion of salmonella infected individuals (line) received by lab

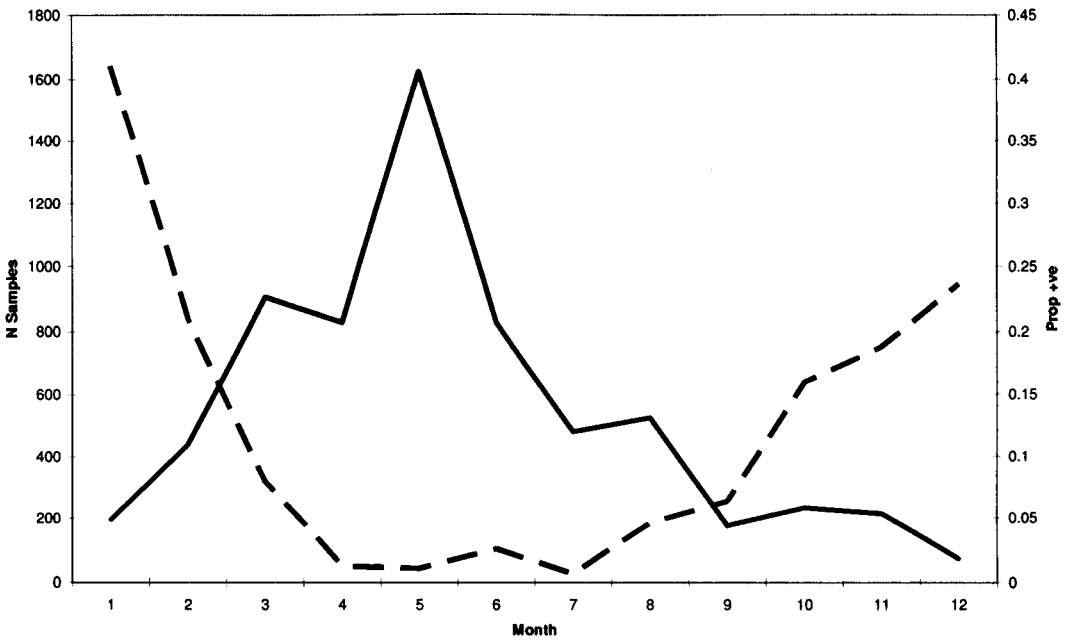


Figure 6.2 Monthly variation in sample size (solid line) and proportion of salmonella infected individuals (hatched line) received each month

tested positive for *Salmonella*, while < 1% of the samples received in Newcastle were found to be infected (Figure 6.1.). There was a pronounced seasonal pattern in salmonella prevalence, with high levels of infection during the winter and much lower levels during the summer (Figure 6.2.).

Canonical Correspondence Analysis

The first axis of the CCA for samples received (Figure 6.3a.) represented a significant trend from West to East (P = 0.002), and a non significant trend of increasing urbanisation (P = 0.080). The samples were distributed along this axis with finches and sparrows having a more westerly distribution, and ducks and swans having a more easterly distribution. The second axis was not related to any of the variables, although there was slight evidence (P=0.118) that it was dependent on rainfall, with gulls present in areas with the highest levels of rainfall, and finches in areas with the lowest levels.

With the effects of sampling partialled out (Figure 6.3b.), salmonella prevalence amongst species was distributed along the first axis, again representing a significant Easterly trend (P = 0.006). In this instance salmonella prevalence in swans and gulls increased with this Easterly distribution. The second axis represented an increasing, but non-significant, trend in the winter minimum temperature (P = 0.084). Here, salmonella prevalence increased in pigeons and ducks, as the winter minimum temperature increased.

Survival Analysis

A survival curve (Figure 6.4.), representing the avoidance of *Salmonella* "events" in each of the labs over time, plotted on a log scale, declines rapidly indicating that by day 75, all regional laboratories had received at least one salmonella infected individual. The parsimonious model (Table 6.2.) for all species indicates that "events" were more likely to involve passerines than non-passerines ($p<0.001$). There was a tendency for events to be dependent on season, with greater prevalence during the winter than the summer ($p=0.079$). *Salmonella* was highest in regions with large numbers of cattle ($p<0.001$), and where a large proportion of land cover is grass ($p<0.001$). A significant negative interaction between cattle and grass cover ($p<0.001$) may indicate that the risk is related to stocking density.

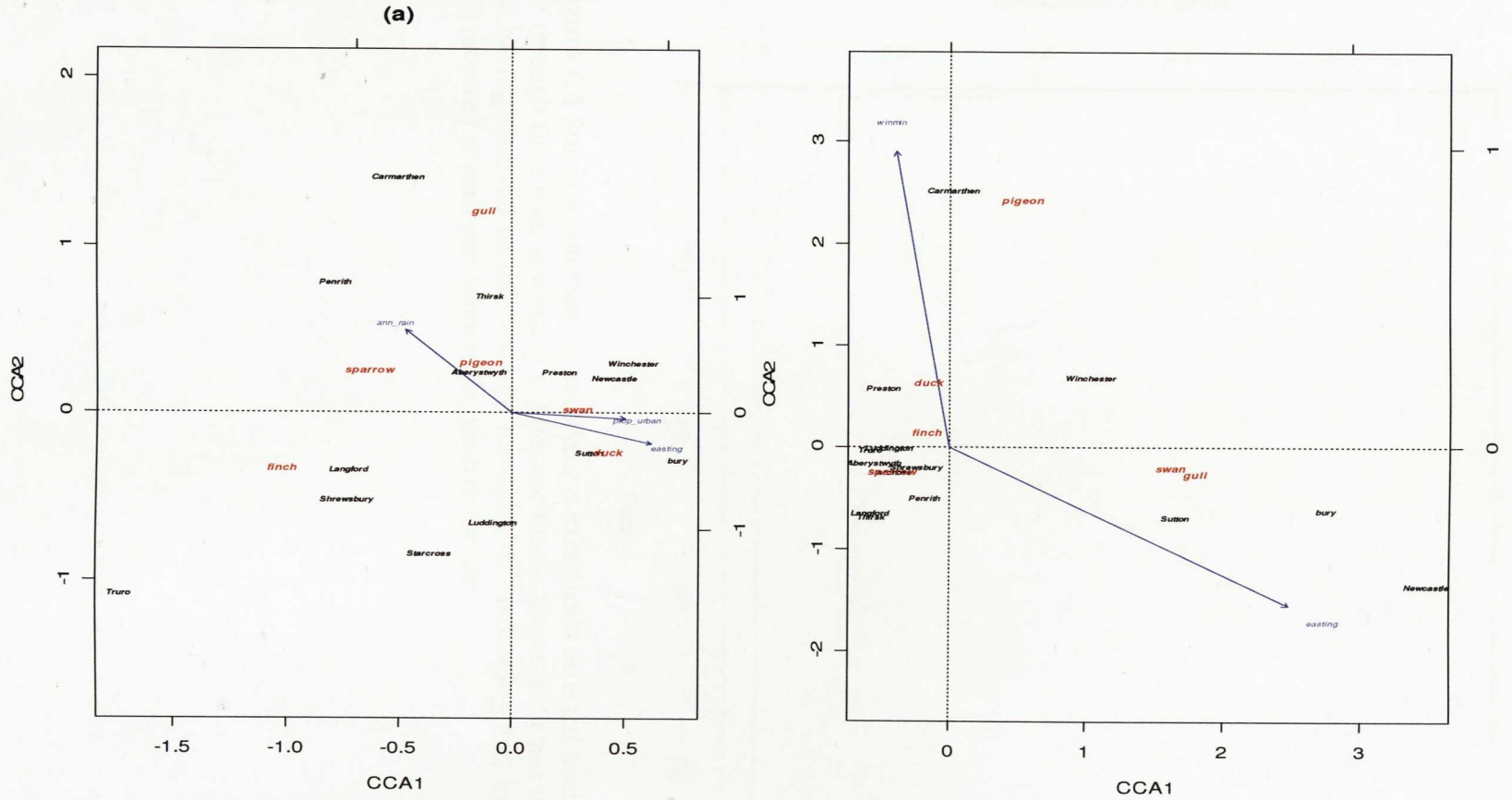


Figure 6.3 Most parsimonious Canonical Correspondence Analysis of (a) distribution of samples received and the effects of annual rainfall (ann_rain), easting and proportion of urban land (prop_urban) AIC 50.96, here the first axis is strongly correlated with an increasingly urban environment and the second axis is weakly related to increasing rainfall, and (b) geographical variation in salmonella prevalence by species and the effects of minimum winter temperature (winmin) easting, with the effect of sampling partialled out, AIC -7.02, here the first axis represents a trend from west to east, whilst the second axis represents a a trend of increasing winter temperature.

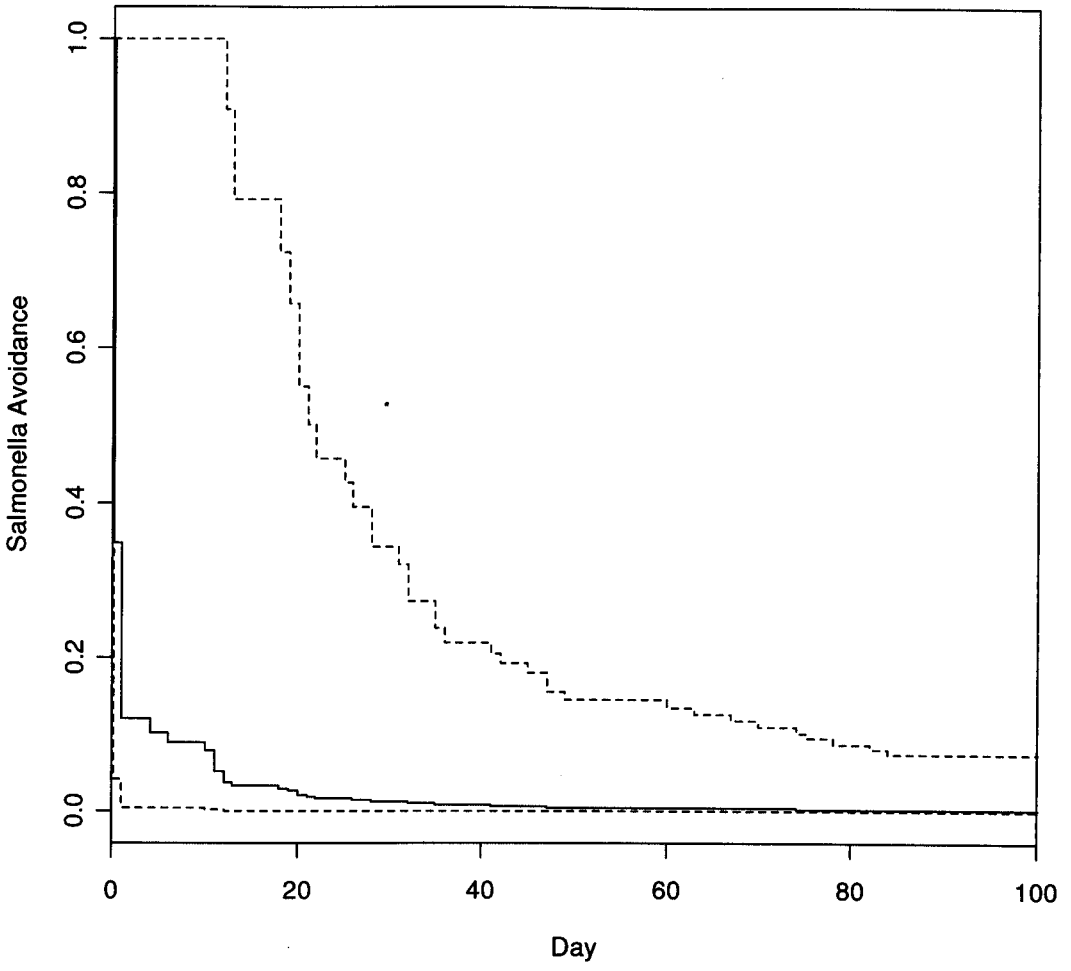


Figure 6.4 Survival function for receiving a salmonella infected bird at each regional lab through time with associated confidence limits. Curve indicates the probability of not having received an infected bird through time, indicating that by day 70 all labs had received at least one salmonella positive sample.

	Model Diagnostics				χ^2 test for non-proportionality		
	Coefficient	Robust SE	Z	P	Rho	χ^2	P
Northing	2.22×10^{-6}	1.36×10^{-6}	1.63	0.100	0.034	0.272	0.602
Passerine	1.31	0.23	5.66	<0.001	-0.019	0.689	0.793
Summer	-0.34	0.19	-1.76	0.079	0.026	0.159	0.690
Cattle	0.07	0.02	3.52	<0.001	-0.023	0.116	0.733
Grass	0.05	0.01	3.32	<0.001	-0.047	0.496	0.481
Cattle x Grass	-0.01	3.88×10^{-4}	-3.61	<0.001	0.056	0.689	0.406
Winter Min Temp	1.03	0.41	2.46	0.014	-0.027	0.172	0.678
Summer Max Temp	0.69	0.22	3.09	0.002	0.111	2.855	0.091
				Global	NA	5.980	0.649

Table 6.2 Regression diagnostics and χ^2 tests for non-proportionality for parsimonious Cox proportional hazards model of salmonella infection at each of the 14 VLA regional labs. R^2 0.364, AIC 990.07, Likelihood ratio test 103 on 8 degrees of freedom, p <0.001, Wald test 75.4 on 8 degrees of freedom, p <0.001

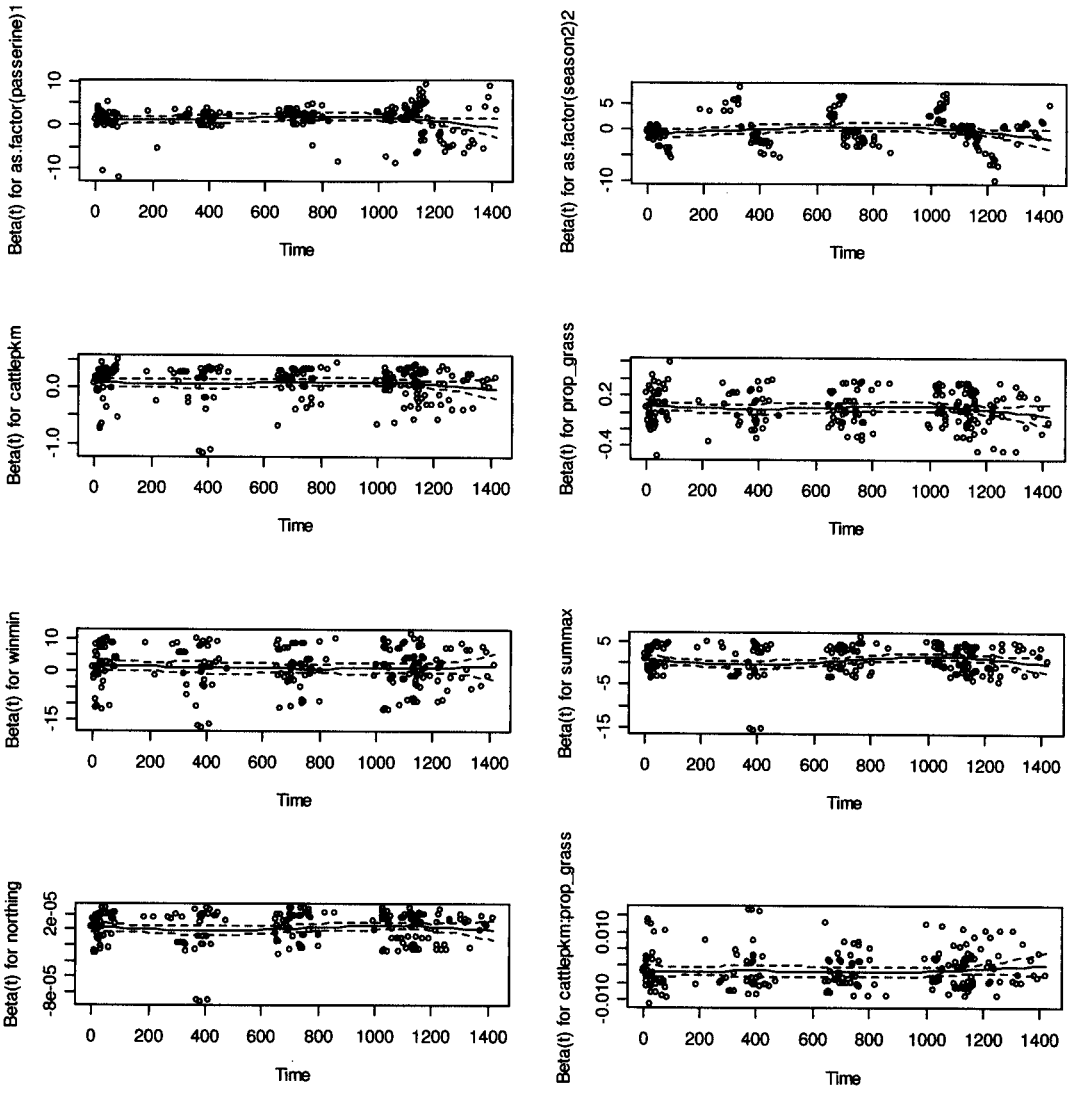


Figure 6.5 Plot of time dependant coefficients for each covariate against time (in days) for the most parsimonious model for salmonella infection data. Note the horizontal nature of the line in each plot indicative of proportionality of effects.

Plots of time dependent coefficients against time were flat suggesting that there was no time dependence in the covariates (Figure 6.5), and tests for non-proportionality were insignificant, indicating that the assumption of proportional hazards was valid (Table 6.2). Analysis of data for passerine families produced a similar result to that for all families (Table 6.3), repeating the seasonal pattern, and with similar responses to

	Model Diagnostics				χ^2 test for non-proportionality		
	Coefficient	Robust SE	Z	P	Rho	χ^2	P
Easting	5.08×10^{-6}	2.32×10^{-6}	2.19	0.029	0.046	0.426	0.513
Winter Min Temp	0.951	0.448	2.12	0.034	-0.026	0.134	0.713
Summer Max Temp	0.251	0.152	1.65	0.098	0.129	3.217	0.072
Cattle	0.112	0.024	4.51	<0.001	0.084	1.377	0.240
Grass	0.115	0.025	4.50	<0.001	0.092	1.706	0.191
Cattle x Grass	-0.002	5.31×10^{-4}	-3.76	<0.001	0.002	0.603	0.975
Summer	-0.754	0.201	-4.39	<0.001	-0.055	0.001	0.437
				Global	NA	9.824	0.198

Table 6.3 Regression diagnostics and χ^2 tests for non-proportionality for parsimonious Cox proportional hazards model of salmonella infection of passerines at each of the 14 VLA regional labs. R^2 0.303, AIC 841.74, Likelihood ratio test 71 on 7 degrees of freedom, p <0.001, Wald test 64.8 on 7 degrees of freedom, p <0.001

cattle and grass. In contrast to the model for all species, passerines demonstrated a significant Easterly trend in their susceptibility to *Salmonella*. As a result of the temporal distribution of *Salmonella* positive samples, it was only possible to consider non-passerine species collected during the final year of the study. Although the analysis appeared to suggest that gulls were more susceptible to *Salmonella* than other non-passerines, it is not possible to draw conclusions from this model as it failed tests for non-proportionality (Table 6.4.).

	Model Diagnostics				χ^2 test for non-proportionality		
	Coefficient	Robust SE	Z	P	Rho	χ^2	P
Northing	7.52×10^{-6}	2.88×10^{-6}	-2.58	0.009	-0.071	0.244	0.621
Summer Max Temp	-1.27	0.54	-2.33	0.020	-0.222	2.537	0.111
Grass	-0.09	0.03	-3.15	0.002	-0.231	2.843	0.0918
Gull	1.33	0.54	2.44	0.015	0.117	0.717	0.390
Pigeon	1.33	0.81	1.64	0.100	-0.237	1.967	0.160
Summer	-2.32	0.82	-2.81	0.005	0.165	1.030	0.310
Autumn	-5.06	1.14	-4.44	<0.001	0.180	1.255	0.262
				Global	NA	19.095	0.008

Table 6.4 Regression diagnostics and χ^2 tests for non-proportionality for parsimonious Cox proportional hazards model of salmonella infection of non-passerines at each of the 14 VLA regional labs.R^2=0.633, AIC 127.67, Likelihood ratio test 47.1 on 7 degrees of freedom, p <0.001, Wald test 28.3 on 7 degrees of freedom, p <0.001

Discussion

By using CCA and survival analysis it was possible to circumvent problems related to sample size faced by previous studies and to provide statistical support for three hypotheses proposed elsewhere. Firstly, there is seasonal variation in the prevalence of salmonella in wild birds (i. e. Refsum *et al.* 2002; Pennycott *et al.* 2006; Hughes *et al.* 2008), secondly, passerines have a higher susceptibility to salmonella than non-passerines (i. e. Refsum *et al.* 2002; Hughes *et al.* 2008), and finally, that human behaviour has increased the probability of wild birds becoming infected with salmonella (i. e. Wilson & MacDonald 1967; MacDonald and Brown 1974 Pennycott *et al.* 1998).

Whilst a number of studies have linked salmonella in livestock to outbreaks of the disease in wild birds (Coulson *et al.* 1983; Boqvist & Vagsholm 2005; Pangoli *et al.* 2008), these results indicate that the reverse may also be true. Up to 10% of cattle faeces in the UK may be contaminated with salmonella (Hutchison *et al.* 2004), which can persist in the soil for up to 69 days, dependent on soil type (Platz 1980). The infection can then be picked up by wild birds either through direct contact with salmonella in the soil, or by feeding on invertebrates which can also carry the infection (Davies & Breslin 2003).

Seasonal variation in wild bird salmonella prevalence may also be driven by human activity. The link between salmonella and artificial sources of food, like landfill sites and garden bird feeders, has been long established (Wilson & MacDonald 1967; MacDonald & Brown 1974). Cases of wild bird salmonella tend to peak during the winter and spring, when reliance on these food sources is at its highest, and large concentrations of birds make use of these artificial feeding stations, This, in combination with harsher conditions, is likely to make birds more susceptible to the effects of salmonella.

There was a significantly higher rate of salmonella in passerines than there was in non-passerines. There are two possible explanations for this. Firstly, there may genuinely be a higher rate of salmonella infection in passerines, or secondly, passerines may be more likely to succumb to the effects of salmonella and therefore this relationship is the result of sampling bias. Comparable levels of salmonella have been found in previous studies involving the collection passerine carcasses (Refsum *et*

al. 2003; Pennycott *et al.* 2006), and salmonella is a major cause of death amongst passerines (Pennycott *et al.* 1998). Whilst there are few studies of salmonella in live passerines, they indicate that the incidence in the population as a whole may be much lower (Refsum *et al.* 2003; Grant *et al.* 2006) and absent amongst migrating birds (Hernandez *et al.* 2003; Palmgren *et al.* 2008)

In contrast, the majority of studies on non-passerines have sampled live individuals, and have tended to focus on gulls, in which estimates of salmonella incidence range from 2.7% (Palmgren *et al.* 2005) to 9.8% (Monaghan *et al.* 1985). Tests on other groups, for example raptors, pigeons and waterfowl, have also produced low estimates of salmonella incidence (Fallacara *et* al. 2001; Reche *et al.* 2003; Lillehaug *et al.* 2005). Whilst our study found a higher incidence of salmonella than has been reported previously, this is likely to be the result of sampling dead birds, and it remains substantially lower than that of passerines. Further evidence suggests that salmonella infection in gulls can be short lived, and does not impinge on migration (Palmgren *et al.* 2006, 2008).

These results imply that salmonella is a more important cause of mortality in passerines than non-passerines. They also have implications for the possible risk of the transmission of salmonella to humans and livestock. Outbreaks of salmonella in passerine species are likely to be short-lived and highly localised. It may therefore be relatively easy to contain them, and to prevent transmission to humans and livestock. In contrast, many non-passerine species appear to be clinically unaffected by salmonella infection, allowing them to spread it over greater distances. This in combination with the persistence of salmonella at colonies between breeding seasons

(Literak *et al.* 1996) may mean that, despite its lower incidence, salmonella in non-passerine species poses a greater risk of zoonotic transmission than salmonella in passerine species.

Chapter 6: An evaluation of techniques to control problem bird species on landfill sites

Abstract

Birds feeding on landfill sites cause problems in terms of nuisance to neighbours flight safety, a threat to public health and affect the day to day site operation. A number of control measures exist to deter problem species, however, research into their effectiveness across sites and for multiple species has been limited. We use a modelling approach in order to assess the effectiveness of 9 techniques – pyrotechnics, hand-held distress calls, static distress calls, blank ammunition, a combination of blank and lethal use of ammunition, the use of falcons, the use of hawks, wailers and helium-filled bird scaring kites - at deterring three commonly recorded species – the Black-headed Gull (*Larus ridibundus*), the Herring Gull (*Larus argentatus*) and the Lesser Black-backed Gull (*Larus fuscus*) – from six landfill sites across the United Kingdom. The use of distress calls, falconry and combinations of lethal and non-lethal use of ammunition were the most effective techniques for initially deterring birds from these sites. However, when habituation is considered there is a clear difference between techniques such as falconry which have a lethal aspect, which may act to reinforce the deterrence, and the use of techniques such as distress calls which do not. However there are problems related to legislation and public perception when lethal techniques are used.

Introduction

Landfill sites often host feeding assemblages consisting of a large number of birds of a relatively small range of species, notably gulls. These feeding assemblages pose a number

of problems, both economically and to public health, within a landscape context. Gulls pose a risk to aircraft (Blokpoel 1976; Burger 2001; Baxter 2003) and can interfere with the daily operation of landfill sites. In addition they have been found to carry a range of pathogens, harmful to both humans and livestock, such as *Salmonella* (Monaghan *et al.* 1985; Ferns and Mudge 2000; Palmgren *et al.* 2006), *Campylobacter* (Broman *et al.* 2002), the avian flu virus H5N1 (Ellis *et al.* 2004), *Esherichia coli* 0157 (Wallace *et al.* 1997) and the infectious bursal disease virus (Hollmen *et al.* 2000). Given the large numbers of birds gathering at these sites and their subsequent dispersal throughout the landscape, the potential for large scale transmission of disease is great.

The annual cost of bird control at a site in the UK can range between US$65-120 000, depending on the scale and methods used (Allan 2002). Given the expense and the potential problems associated with the presence of gulls on landfill sites, it is important to investigate the effectiveness and limitations associated with a range of different control techniques. These techniques can be split into 2 groups, those that involve large-scale population reduction, removing the problem permanently, and those that merely aim to deter birds. A number of large-scale culls of gulls have been attempted (i.e. Bosch *et al.* 2000; Guillemette and Brousseau 2001; Finney *et al.* 2003). However, attempts at controlling populations at a large scale have often failed due to the immigration of individuals from neighbouring populations and the need to apply the methods consistently across the whole population and dispersal of individuals within the landscape (Bosch *et al.* 2000). Such large scale population control is also often controversial and may encounter legal obstacles, e.g. bird protection legislation.

While many studies have looked at the impacts of lethal control at a population level, few have looked at the impacts on bird abundance at individual sites. John F Kennedy Airport

in New York initiated a program of shooting gulls flying over its runways in 1991 (Dolbeer *et al.* 1993). This was highly successful in reducing the number of bird strikes with aircraft. However, there has been some debate as to whether the mechanism for this reduction is the deterrent effect of the shooting or an overall reduction in population size (Brown *et al.* 2001).

Other tactics have also been used to deter birds from problem areas. Some of these such as the use of birds of prey (summarized by Ericson *et al.* 1990) have a limited lethal aspect, but have proven to be highly effective at keeping problem species away from areas such as airports (i.e. Blokpoel 1977). However, there are a number of limitations on their usage such as cost and the prevailing climatic conditions. A number of non-lethal control techniques have also been developed. These include distress calls (i.e. Delwiche *et al.* 2005), lasers (Gorenzel *et al.* 2002), pyrotechnics (Olijynk & Brown 1999), fogging (Vogt 1997) and mylar flags (Belant & Ickes 1997). All studies found that while these techniques could be effective in dispersing flocks of birds causing a problem, they were subject to varying degrees of habituation, where birds become accustomed to, and subsequently ignore, the intervention (Bomford & O'Brien 1990; Andelt & Hopper 1996; Olijynk & Brown 1999).

In order to compare the efficacy of a range of control methods, it is important to examine their effectiveness at a range of sites. Whilst studies investigating the effectiveness of

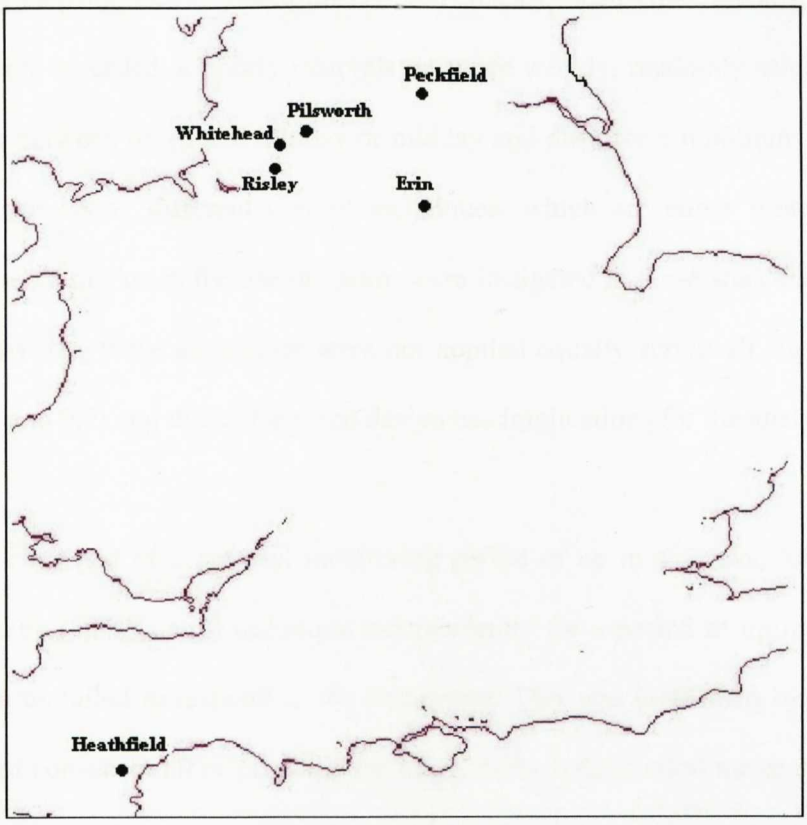


Figure 1 Locations of Landfill sites used in study

these control methods have been compared (Gilsdorf *et al.* 2002), no single study had examined the application of multiple techniques to multiple sites. Using a combined field observational and modelling approach, this study examines the responses of three species, the Herring Gull (*Larus argentatus*), the Lesser Black-backed Gull (*Larus fuscus*) and the Black-headed gull (*Larus ridibundus*), to a variety of control methods at six landfill sites in the United Kingdom.

Methodology

Count data from the six UK landfill sites shown in figure 5.1 were collected between 1999 and 2001. Regular supplies of domestic waste were deposited at each site (at least 250 000 tonnes per annum). The sites were characterised by being on the edge of towns and surrounded by large areas of farm and grass land. During the study period the

numbers of Herring, Lesser Black-backed and Black-headed Gulls feeding or loafing on the sites were recorded at hourly intervals on twice weekly, randomly selected sampling days either between dawn and midday or midday and dusk for a minimum of 6 hours on each occasion. Nine different control techniques, which are either routinely used on landfill sites or marketed for use on them, were instigated at these sites during the study period. However, these techniques were not applied equally across all sites and months (tables 5.1 and 5.2) and this unbalanced design has implications for the analysis

Each trial consisted of a pre-trial monitoring period of up to 4 weeks, followed by the implementation of a control technique independently for a period of up to 12 weeks, or until the birds failed to respond to the deterrence. This was confirmed by a morning or afternoon of consistent nil response by the target birds to the control measure.

Trials were conducted as follows. Where bird scaring kites were used, 3 were deployed over the site for the study period. Pyrotechnics and distress calls were deployed "on demand" when birds were seen attempting to land. However, due to economic considerations, the use of pyrotechnics was limited to a maximum of once every 15 minutes. The distress calls of Black-headed Gulls and Herring Gulls were used depending on which species constituted the majority of the count. Where this was the Lesser Black-backed Gull, Herring Gull distress calls were used.

In trials of falcons, hawks and the lethal use of ammunition, gulls were targeted under Schedule 2 of the 1981 UK Wildlife and Countryside Act (as amended). Specific licenses were held under section 16 of the Act (WLF100085) for targeting Black-headed gulls. All hawks and falcons used in these studies were registered with the UK Department for

	Hawks	Falcons	Distress Calls	Helium filled kites	Blank ammunition	Pyrotechnics	Wailers	Static Distress	Blank and Lethal Ammunition	Total trials at site
Peckfield	2	3	2	1	1					9
Pilsworth	1	2	2	1			1		1	6
Heathfield	1	1	1	1		1			1	6
Whitehead	2	2	2		1					7
Erin	1	1	1		1			1		5
Risley		1	1		1					3
Number of trials for each technique	7	10	9	3	4	1	1	1	2	36

Table 5.1 The distribution of trials throughout the study period by site and control technique.

	January	February	March	April	May	June	July	August	September	October	November	December
Hawks		2000			1999			2000		2000	1999	1999,2000
Falcons	2000, 2001	2001	2000	2000		1999, 2000			1999(2), 2000			
Distress Calls	2000, 2001	2000				1999, 2000		1999	2000(2)		1999	
Bird Scaring Kites				1999			1999					1999
Blank Ammunition			2000(2)				2000(2)					
Pyrotechnics					2000							
Wailers								2000				
Static Distress Calls											2000	
Blank and Lethal Ammunition	2001	2001										

Table 5.2 Distribution of trials in each month and year, where trials of the same technique ran concurrently, number of trials indicated in ()'s

Environment, Food and Rural Affairs under license 14008. Any carcasses were removed from the site. Up to 3 hawks or falcons were used at each site, although they were always flown independently. Their deployment was predominantly limited by weather, with hawks not flown in winds >33 km/h and falcons not flown in winds >46 km/h. Neither was flown during rain or fog.

The resulting data were used to construct a series of linear mixed-effects models for each trial period using the nlme extension in R (Pinheiro & Bates 2000). This method has the advantage of making a parsimonious model allowing cross-species comparisons, while also allowing the analysis of unbalanced data. By treating variables, such as species, as random effects, fewer degrees of freedom are used as the individual intercepts and coefficients for each species are treated as deviations from the mean population (Pinheiro and Bates 2000).

In order to normalise the count data it was log transformed and assessed using a quantile-quantile plot. Species, the presence of control, time of day and day number were included in the full model as fixed effects. In addition interactions between control and time, species and day number were considered. Time was sine- and cosine-transformed in order to take account of the daily variation in behaviour displayed by the study species. Control, species and day number were also included in the full model as random effects. An AR(1) correlation structure, where adjacent observations have a higher correlation than non-adjacent observations, was included in the model to account for temporal autocorrelation. The models were constructed by dropping each factor sequentially and comparing the resulting model to the full model using a likelihood ratio test. When the two models differed significantly, the one with the lowest Aikaike Information Criterion (AIC) was chosen (Burnham and Anderson 1998). When comparing models in which the fixed

effects differed, maximum likelihood (ML) was used, as comparing models in which the fixed effects vary using restricted maximum likelihood (REML) produces results which are not interpretable (Pinheiro and Bates 2000). For all other models REML was used.

The final most parsimonious models were assessed for temporal autocorrelation, and checked, using quantile-quantile plots and plots of fitted against observed values, to ensure assumptions of normality were met. The parameters were then used to calculate the initial effectiveness of each control method, as well as the rate at which the study species habituated to each technique. The initial effectiveness of each technique was taken as being the percentage drop in the number of birds present at 1200 hours, on the day before and the day after control commenced. The degree of habituation to each technique was taken as the gradient of the slope of the fitted values between the commencement of the control and the end of the study period. The effects of month and trial number on both the initial effectiveness and degree of habituation were then investigated for each species using a linear regression. Month was sine and cosine transformed in order to allow for seasonal variation in the behaviour of the study species. The effects of site were investigated using analysis of variance. All analyses were conducted in R (R Development Core Team 2005).

Results

The number of gulls present on the landfill sites peaked around midday, the mean and maximum numbers of each species present at this time with no control present are shown in table 5.3. The length of the trials varied from 18 days for the helium filled kites at Heathfield to 128 days for falcons at Whitehead (table 5.4).In trials of control with a lethal aspect, 322 gulls were shot, 31 were taken by falcons and 12 were caught by hawks.

	Herring Gull		Black Headed Gull		Lesser Black-backed Gull	
	Mean	Maximum	Mean	Maximum	Mean	Maximum
Peckfield	17.09 (+/-3.48)	490	165.22 (+/-21.95)	2450	26.40 (+/-4.05)	583
Pilsworth	53.88 (+/-11.81)	1900	69.40 (+/-12.33)	1150	196.53 (+/-26.27)	3154
Whitehead	80.75 (+/-17.04)	1425	119.18 (+/-16.90)	1310	64.45 (+/-10.56)	1395
Heathfield	2074.67 (+/-159.21)	7450	456.23 (+/-63.92)	3250	3.13 (+/-0.47)	32
Erin	50.89 (+/-13.96)	1238	151.63 (+/-35.72)	3700	94.39 (+/-16.31)	1302
Risley	39.76 (+/-14.99)	2050	49.63 (+/-11.84)	1360	24.17 (+/-5.46)	542

Table 5.3 Mean and Maximum numbers of each gull species observed at study sites at 12 noon. For mean values Standard Errors shown in brackets.

In addition 315 corvids were shot, 106 corvids and other birds were taken by falcons and 57 corvids and other birds were taken by hawks. There was a great deal of variation in the initial change in gulls numbers at the start of control, however this did not differ significantly between sites (figure 5.2, $P>0.05$) and most of the variation is likely to be due to differences between techniques and the effects of the covariates.

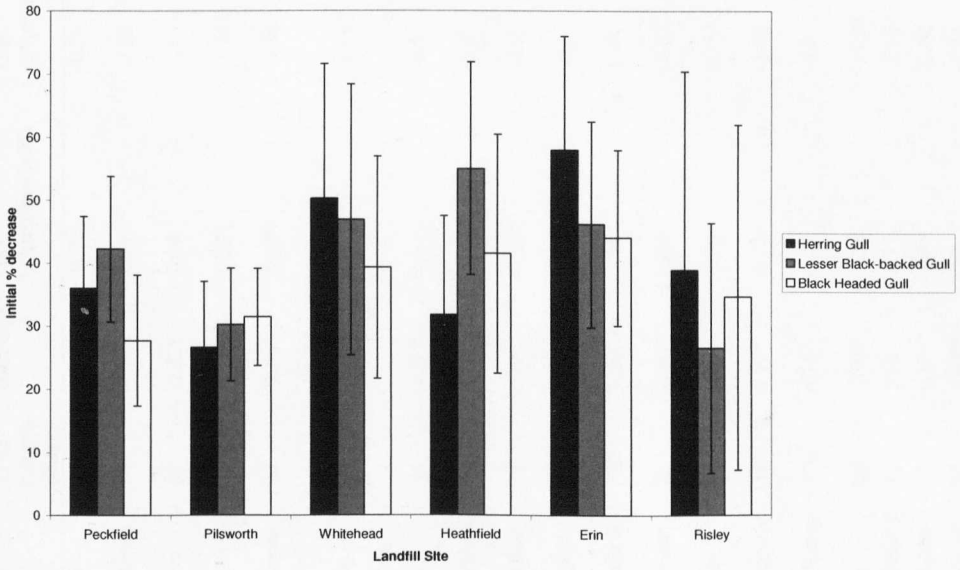


Figure 5.2 Initial % decrease in bird numbers between 12 noon on the day before and after commencement of control at each landfill site (+/- Standard Error)

Control	Site	Trial Length (Days)	Intercept	Sin (2*pi*time/2400)	Cos (2*pi*time/2400)	Control	Day	Species	Sin(2*pi*time/2400) control	Cos(2*pi*time/2400) control	Control day	Control species	D^2 (Deviance explained)
Blank ammunition	Erin	44	1.27	-0.26*	-0.58	-0.66							0.75
Blank Ammunition	Peckfield	81	-2.14	-0.19*	-2.02	-0.25*		1.30*					0.52
Blank Ammunition	Risley	63	-1.22*	-0.96	-3.63	3.53	0.04*		-0.25*	1.28	-0.06*		0.63
Blank Ammunition	Whitehead	104	-0.06*	-0.22*	-3.16*	1.4		0.70*	-0.20*	1.34		-0.58	0.42
Blank and lethal ammunition	Pilsworth	20	-2.54*	-0.90*	-9.36	2.92	-0.07		0.08*	4.1			0.83
Blank and lethal ammunition	Pilsworth	59	-11.28	-3.3	-13.42	8.12	0.48*		1.01*	5..39	-0.41		0.61
Distress Calls	Erin	75	-0.86*	0.64*	-8.3	2.14	-0.04		-0.2	4.01			0.49
Distress Calls	Heathfield	103	9.2	-0.72	-1.8	-4.13	-0.01*	-2.70*			0.02	0.61	0.69
Distress Calls	Peckfield	63	0.79*	-0.26*	-2.55	-0.45*							0.55
Distress Calls	Peckfield	71	0.73	-0.24*	-0.6	-0.51							0.34
Distress Calls	Pilsworth	122	7..50	-1.94	1.93	-6.68	-0.04*	0..51*	1.03	-3.03	9.4		0.71
Distress Calls	Pilsworth	27	-1.82*	1.96*	-7.23	0.93			-1.75	2.20*			0.76
Distress Calls	Risley	86	9.45	-1.93	0.15*	-8.23	-0.11		0.78	-0.50*	0.12		0.65
Distress Calls	Whitehead	113	1.17*	-0.22*	-2.02	-1.16*	-0.04	1.72*	-0.45	0.8	0.03	-0.6	0.54
Distress Calls	Whitehead	106	6.84	-2.1	-3.7	-3.3		-1.73*	0.72	1.85		1.03	0.77
Falcons	Erin	66	-0.95*	-1.32	-11.84	0.35*	-0.25		0.7	5.72	0.13		0.57
Falcons	Heathfield	107	2.88	-0.77	-2.13	-0.76	-0.01						0.58
Falcons	Peckfield	115	0.13*	-1.99	-3.02	-0.33*	-0.18	1.81*	1.05	1.16	0.09	-0.7	0.62
Falcons	Peckfield	95	-0.64*	-0.54	-1.84	0.81	-0.01*		0.27	0.63	-0.01		0.37
Falcons	Peckfield	42	2.39	-0.33*	-1.07	-0.40*	-0.07						0.47
Falcons	Pilsworth	109	6.15	-1.96	-1.72	-1.87	-0.01	-1.82*	0.72	0..53*		0.84	0.68
Falcons	Pilsworth	106	2.11	-1.43*	-4.44	-0.33*	-0.04		0.29*	2..54*	0.01		0.61

Falcons	Risley	112	0.22*	-2.01	-2.16	-0.56	0.02		0.73	0.73			0.54
Falcons	Whitehead	128	0.08*	-0.93	-5.15	0.70*	0.01		0.38	2.79	-0.01		0.5
Falcons	Whitehead	74	4.44	0.88	-5.08	-1.95	-0.14		-0.43*	2.3	0.06		0.67
Hawks	Erin	109	-1.74*	-0.03*	-3.8	2.31*	0.04				-0.04		0.94
Hawks	Heathfield	102	2.85*	-1.6	-4.28	-0.03	-0.51*		0.43*	1.18	0.01*		0.32
Hawks	Peckfield	63	0.49*	-0.22*	-1.61	-1.17		0..35*					0.51
Hawks	Peckfield	72	0.01*	0.02*	-2.57	-0.72							0.57
Hawks	Pilsworth	68	-0.32*	0.41*	-5.36	1.72	-0.03*		-0.27*	1..90			0.63
Hawks	Whitehead	75	5..99*	1.15	-2.61	-3.06	0.06	-1.09*				0.79	0.74
Hawks	Whitehead	81	0.81*	-1.84	1.01*	-0.72*	0.03		0.94	-2.29			0.4
Helium filled kites	Heathfield	18	2.61*	0.85	-2.77	-0.62*	0.02*						0.84
Helium filled kites	Peckfield	57	-1.88	-0.68	-2.33	-0.94*	1.64*						0.68
Helium filled kites	Pilsworth	48	1..91*	-1.1	-2.01	-1.04*	0.03*						0.64
Pyrotechnics	Heathfield	78	9.54	-1.27	-2.32	-3.13	-0.04	-2.93	0.32	0.3	0.03	0.49	0.69
Static Distress Calls	Erin	97	-1.10*	0.984*	-5.58	1.64*	-0.02	0.74	-0.06*	2..96			0.53
Wailers	Pilsworth	25	-2.94*	-1.28	-3.95	3.76	0.11*	1.22*	-0.20*	1.63	-0.1	-0.69	0.66

Table 5.4 The parameters for the most parsimonious models of each trial, *=insignificant variable however, likelihood ratio tests supported inclusion of variable in final model, also reported are the values for D^2 and length of study period.

The most parsimonious models considered day nested within species as random effects. All models met assumptions of normality and showed little or no evidence of temporal autocorrelation. The most parsimonious models are presented here (Table 5.4). In all but 6 trials, the application of control had a significant effect on the number of birds present. Hand held distress calls, blank ammunition and falcons all failed to have an effect on one of the occasions on which they were deployed however, helium-filled bird scaring kites failed to have a significant effect on any of the 3 occasions on which they were deployed (table 5.4).The patterns of bird abundance during the trial periods could generally be fitted into one of three categories. The first of these is illustrated by the use of falcons at Pilsworth Landfill Site (figures 5.3A and B). Here, whilst the number of gulls on the site was declining initially, the introduction of falcons on day 28 caused a greater decline. The number of birds recorded at the site then continued to drop for the duration of the trial. The use of helium filled bird scaring kites at Heathfield landfill site illustrates a second category (figures 5.4A and B). Here, numbers remain relatively constant both before control was introduced and whilst it was applied. In cases like this, control had little or no impact on the number of birds recorded, and the majority of variation observed in bird numbers resulted from diurnal patterns (Table 5.4). In the final category, the number of birds observed dropped following the commencement of control measures, as seen when pyrotechnics were deployed at Heathfield landfill site (figures 5.5A and B). The number of birds recorded, after control measures were introduced for the first time, then began to rise for the remainder of the trial.

The initial effectiveness (figure 5.6) and rate of habituation (figure 5.7) for each technique varied greatly both within and between methods, and some of this variation will be explained by the model covariates. For all 3 species, distress calls and falcons produced large initial decreases. The use of static distress calls and pyrotechnics also produced

Figure 5.3A

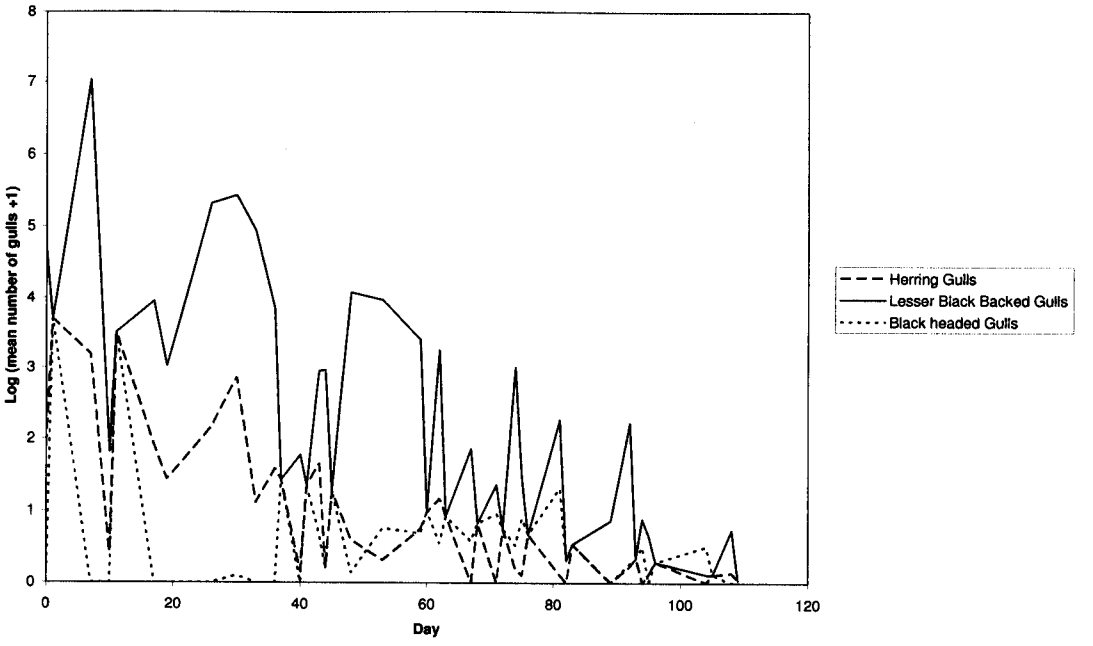
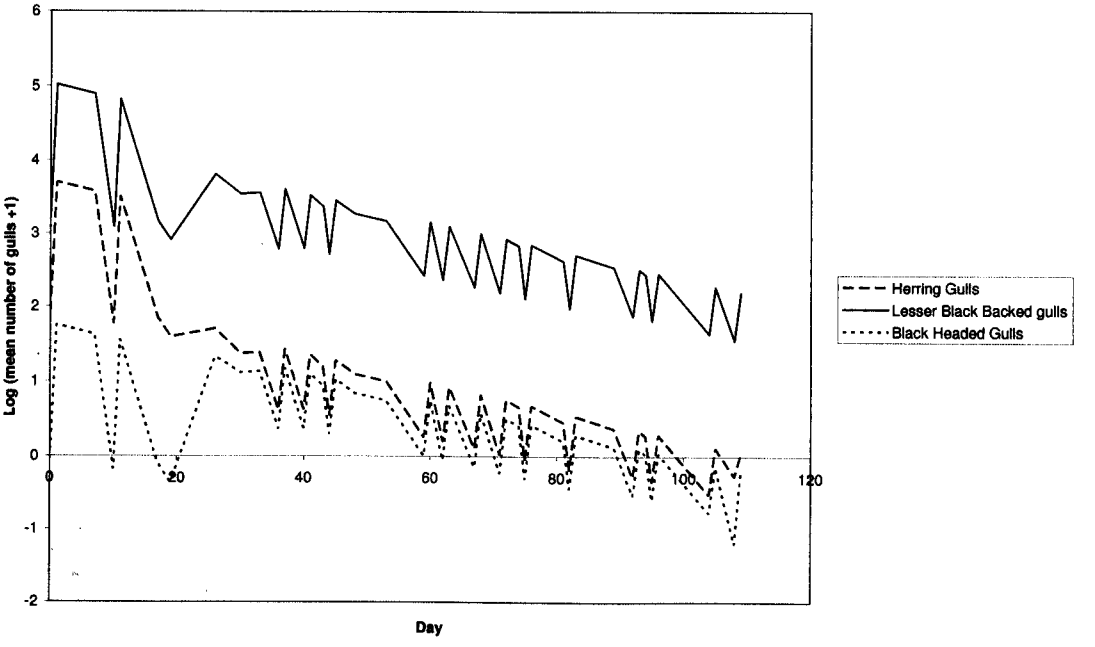


Figure 5.3B



Figures 5.3A and B The observed (a) and fitted (b) values for the trial of falcons at Pilsworth Landfill site starting in June 1999. Days 1-28, pre-control monitoring period, days 28 onwards control applied. $D^2 = 0.68$

Figure 5.4A

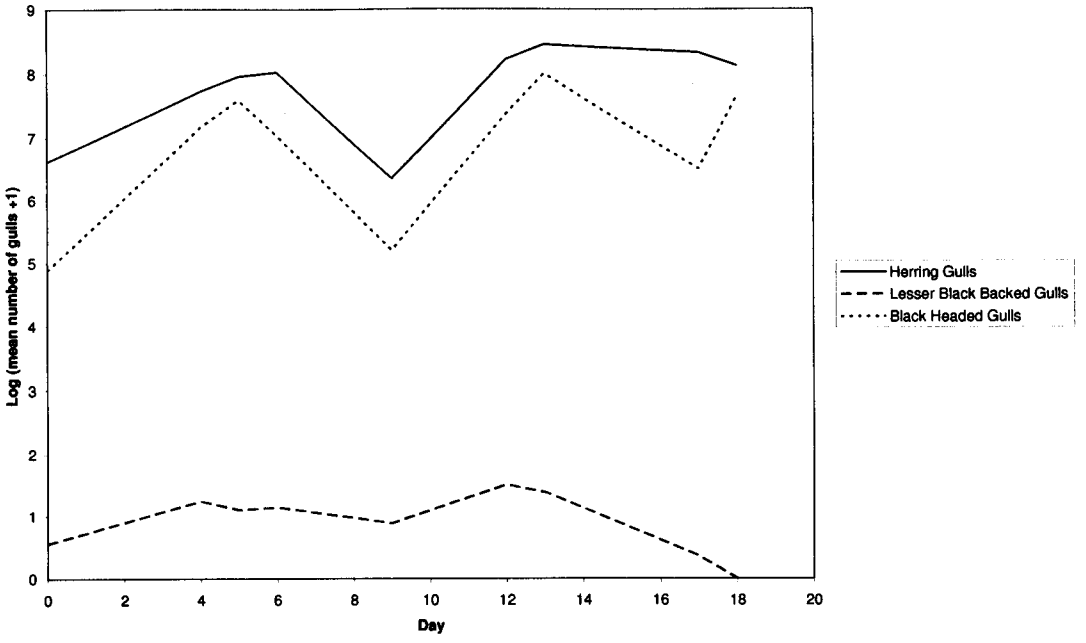
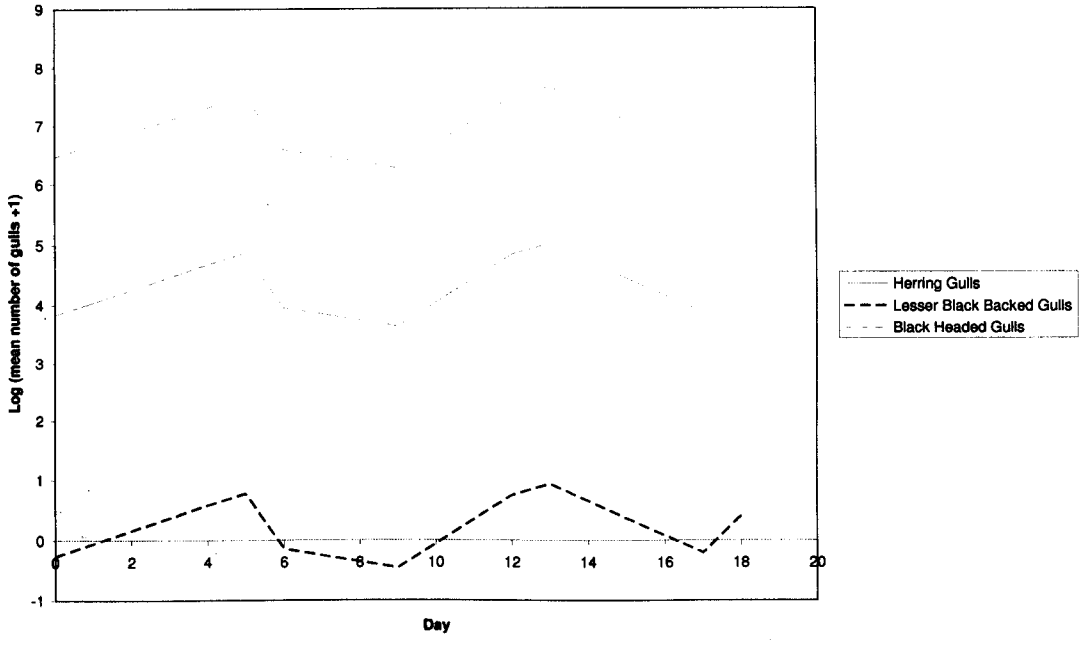


Figure 5.4B



Figures 5.4A and B_The observed (a) and fitted (b) values for the trial of Helikites at Heathfield Landfill site starting in December 1999. Days 1-10, pre-control monitoring period, days 10 onwards control applied. $D^2 = 0.84$

Figure 5.5A

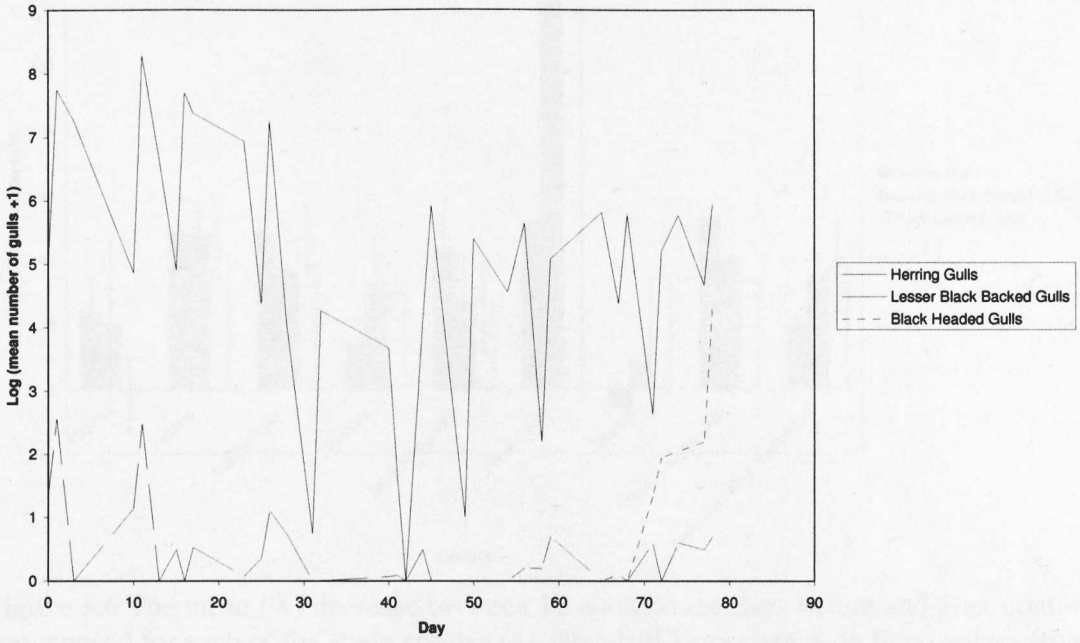
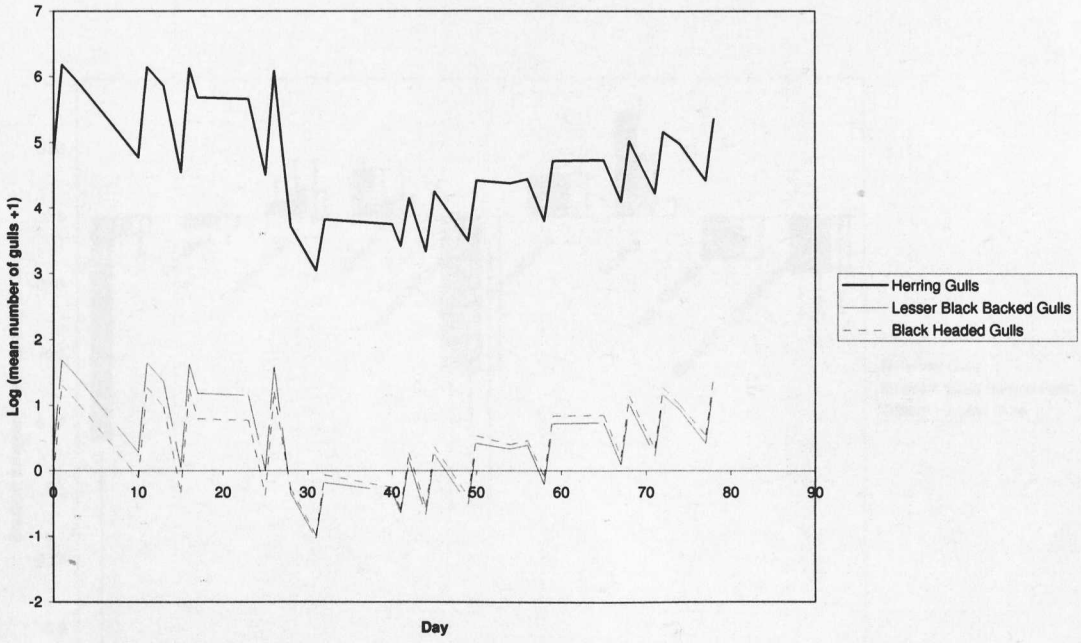


Figure 5.5B



Figures 5.5A and B The observed (a) and fitted (b) values for the trial of Pyrotechnics at Heathfield Landfill site starting in May 2000. Days 1-28, pre-control monitoring period, days 28 onwards control applied. $D^2 = 0.69$

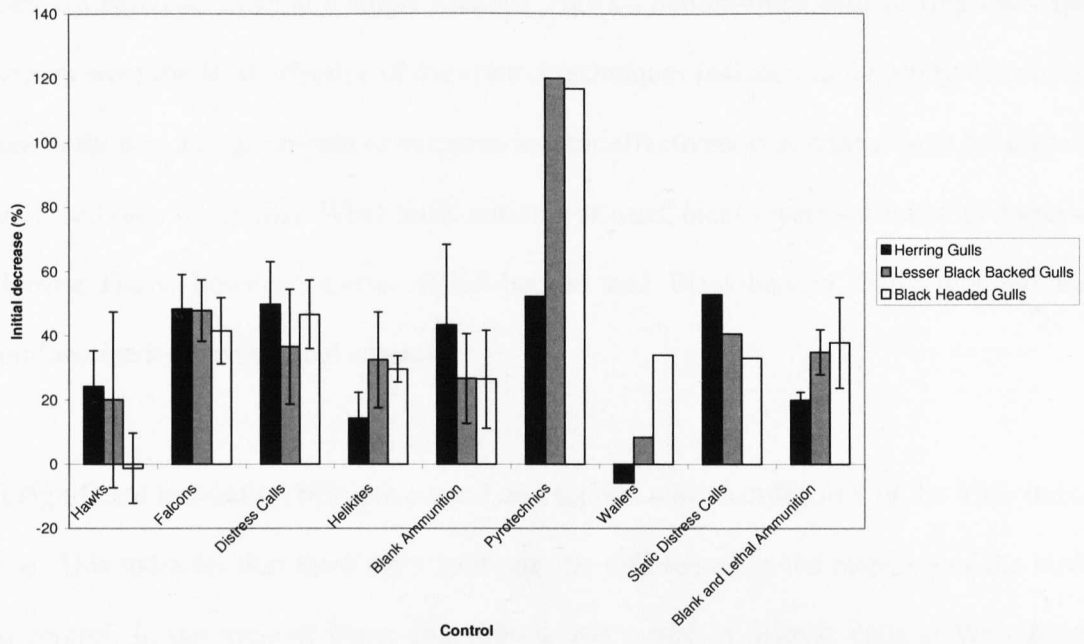


Figure 5.6 The mean (%) decrease between 12 noon on the days before and after control commenced for each of the study species (+/- Standard Error) based on fitted values from models

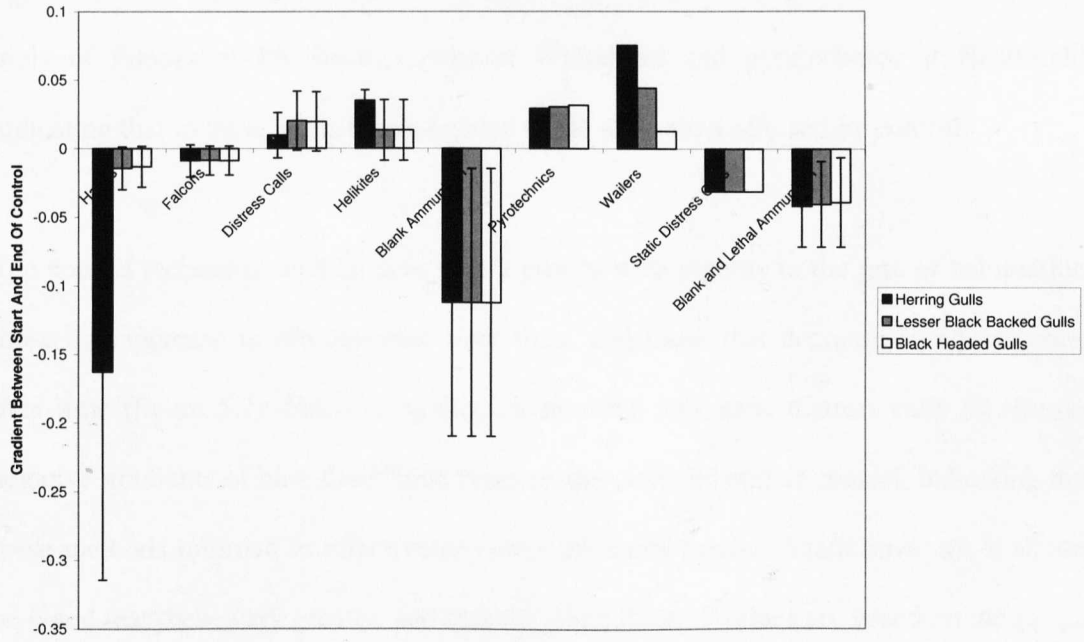


Figure 5.7 The mean gradient between start and end of control for each technique and species (+/- Standard Error) based on fitted values from models.

large decreases among all three species. These results should be treated with caution as they are based on trials at a single location. Hawks, helium-filled bird scaring kites and wailers were the least effective of the control techniques included in the study. However, hawks showed a large amount of variation in their effectiveness and the results for wailers are based on a single trial. When ammunition was used, blanks were sufficient to disperse Herring Gulls, however, Lesser Black-backed and Black-headed Gulls required the reinforcement of some lethal control.

A significant interaction between control and species was recorded in 9 of the trials (table 5.4). This indicates that there were inter-specific differences in the response of the birds to control. In the trials of blank ammunition and a trial of distress calls at Whitehead, falcons at Heathfield and wailers at Pilsworth this relationship was negative, indicating that Herring Gulls were most affected by the control. In a second trial of distress calls at Whitehead and one at Heathfield, the relationship was positive. This was also the case in trials of falcons at Pilsworth, hawks at Whitehead and pyrotechnics at Heathfield, indicating that in these cases Black-headed Gulls were most affected by control.

The control techniques can be split into 2 groups with regards to the rate of habituation, those that increase in effectiveness over time, and those that decrease in effectiveness over time (figure 5.7). Falcons, hawks, ammunition and static distress calls all showed negative gradients of bird abundance between the start and end of control, indicating that these methods improve in effectiveness over the study period. Again however, it should be noted that these vary greatly, and that the static distress values are based on the results of a single trial. The remaining techniques all had a positive gradient between the start and end of control, indicating that they are becoming less effective over time.

Discussion

Of the techniques trialled on more than one occasion, hand held distress calls, the use of falcons and both lethal and non lethal use of ammunition had the greatest initial effect. Of these, the use of falcons, distress calls and a combination of lethal and non-lethal use of ammunition were the most consistent and effective techniques. Whilst distress calls were effective at dispersing all 3 species initially, birds rapidly became habituated to the technique. Lethal techniques, such as the use of falcons and ammunition, which reinforce visual and audio cues with the occasional death of individuals have the opposite effect on habituation and more gulls were deterred as the trial progressed.

There was a difference between the response of the study species to hawks and to falcons. At first glance, this may seem surprising. However, falcons are more successful at capturing gulls than hawks (Baxter and Allan 2006). In addition, falcons tend to fly faster than hawks (Cramp and Simmons 1980) and the gulls may be able to outpace hawks, and therefore do not need to respond as quickly as they do to escape falcons. Two trials involving falcons, and one involving hawks showed inter-specific differences in response to control, likely to result from differences in response to predators. Black-headed gulls showed lower initial decreases in response relative to those shown by both Herring and Lesser Black-backed Gulls. This may be a size related difference as response to predators is positively correlated with an individuals body mass (Fernandez-Juricic *et al.* 2006), with smaller birds, such as the Black-headed Gull, being more agile, and thus able to escape predators more easily.

Distress calls have been widely used to control problem species (i.e. Andelt and Hopper 1996; Baxter 2000; Delwiche *et al.* 2005). As a control, distress calls are often only of use

for a limited period due to the effects of habituation. In addition, it is important to use the correct call. In this study distress calls were more effective at reducing the numbers of Black-headed Gulls and Herring Gulls than they were at reducing Lesser Black-backed Gulls. These differences may be due to the specific nature of distress calls (Boudreau 1968).

The use of pyrotechnics and static distress calls both had promising results for all three species. However, these are based on single trials, and as such further investigation is required before any firm conclusions can be drawn on their general effectiveness. Evidence from previous trials at roost sites provided mixed results (Gosler *et al.* 1995; Olijnyk and Brown 1999). Whilst pyrotechnics can be successful at dispersing gulls from roost sites in combination with distress calls (Gosler *et al* 1995), this relies on the presence of alternative roost sites nearby in order to be effective. When used in isolation over a period of years, pyrotechnics do not reduce the number of gulls at a roost, as a result of habituation (Olijnyk and Brown 1999). A number of studies have found that rotating the use and location of scaring devices, such as pyrotechnics, propane cannons and distress calls, as well as limiting their use to critical times, reduces the rate of habituation (Littauer *et al* 1997; Stevens *et al.* 2000; Ronconi *et al.* 2004; Ronconi and St. Clair 2006)

Of the non-lethal techniques considered in this study audible deterrents such as distress calls are more effective than purely visual methods, such as helium filled bird scaring kites. Other visuals deterrents, such as mylar flags (Belant and Ickes 1997) and models of birds of prey (Conover 1979; Ronconi and St. Clair 2006), have also proved ineffective at deterring problem species. Even when combined with more effective techniques, purely visual stimuli have little impact on problem species (Ronconi and St. Clair 2006).

The number of organisations offering pest control, and in particular control of avian pests, has increased dramatically in recent years in the United Kingdom (BPCA 2006). However, as a result of the difficulties associated with conducting studies on large industrial sites, the focus has tended to be on a limited number of techniques on single sites and the results are often limited to the "grey" literature. In order to identify effective pest management techniques, it is important to collect data from multiple trials at multiple sites. This study illustrates the advantages of a modelling approach for dealing with the complex data that often arises from such a study.

When developing a control strategy factors other than the effectiveness of any techniques need to be taken into consideration, such as public perception. Control of problem species has long been a contentious subject in ornithology (Grinnell 1932; McAtee 1933), and techniques with a lethal aspect are particularly controversial. Recently however, there has been some acceptance by the public, of the need to control problem species and populations. This is especially true when there is a wider understanding of the nature of the problem (White and Whiting 2000; Barr *et al.* 2002). There are also legal implications to consider. General licenses issued in the United Kingdom under the 1981 wildlife and countryside act do not permit the killing of the Black-headed Gull, one of the most commonly observed species on landfill sites and, as for this study, a special license must be obtained. In addition, there are limits imposed on the use of audible deterrents as a result of the 1990 environmental protection act, which has been used to prevent farmers from using such scarers (National Farmers Union 2005). As a result, the legality of any control measures must be taken into account when considering a management strategy on landfill sites.

Using a combination of the techniques that were found to be successful in this study will maximise the effectiveness of pest management schemes. We believe that it is important to both rotate the techniques used, and to use them in combination in order to minimise the effects of habituation. This study found that distress calls, falcons and lethal and non lethal use of ammunition in particular were particularly effective at deterring problem species from landfill sites. However, distress calls were subject to habituation, suggesting that their usage should be limited and strictly on demand. They do, however, remain necessary as constraints imposed by public perception, legislation and climatic conditions are likely to limit the use of more effective techniques, such as falconry, which involves the death of individual birds.

Chapter 7: Discussion: The importance of using ecology to inform management decisions

Gulls pose a variety of problems as a result of their interactions with people. This thesis has highlighted the risk that large gull roosts pose to low-flying aircraft, and that gulls may play a greater role in the zoonotic transmission of *Salmonella* than other non-passerine species. However, managing this risk has often proved difficult. Gulls are a long-lived, aggressive family, which tend to be highly generalist in their choice of both food and habitat (Cramp *et al.* 1983). As a result, predicting their distribution can be difficult, making it difficult to manage their populations.

Effective species management is an important goal for much ecological research, both in the context of conservation of rare species and in the control of pest species. However, many management plans have been ineffective as a result of a failure to appreciate the ecology of the systems concerned. For example, a failure to consider the effects of density dependence has meant that culls of the great cormorant (*Phalacrocorax carbo sinensis*), a piscivorous species often in conflict with fisheries and aquaculture, have had little effect on the overall population size (Frederiksen *et al.* 2001). Attempts to control starlings, *Sturnus vulgaris*, a widespread species responsible for a great deal of agricultural damage, have been hampered by a failure to consider the different spatial scales at which they use the landscape (Clergeau 1995).

In contrast, considering factors such as carrying capacity or life history stage can greatly improve any control strategy. Brook *et al.* (2006) found that by removing

possible nest sites and reducing the access to edible waste in city centres, it was possible to effectively control populations of the house crow, *Corvus splendens*, by reducing the areas carrying capacity. A comparison of attempts to control populations of the mute swan, *Cygnus olor*, showed that reducing adult survival rates was more effective at limiting the overall population than reducing breeding success (Ellis & Elphick 2003).

Attempts to manage problem gull populations have also suffered from a failure to properly appreciate their ecology. The most common form of control used on problem gull populations are a range of techniques used to harass birds when they settle in an area. These techniques include the use of blank and lethal rounds, birds of prey, pyrotechnics and distress calls (Dolbeer *et al.* 1993; Gosler *et al.* 1995; Olijnyk & Brown 1999; Baxter & Allan 2006; Baxter & Robinson 2007; Baxter & Allan 2008; Cook *et al.* 2008; Soldatini *et al.* 2008). However, these methods are often only of use for a limited period due to the effects of habituation.

Elsewhere, gull populations have reached the stage where more drastic measures are necessary. Consequently, to limit colony population sizes individuals are culled and eggs are made unviable (Coulson *et al.* 1982; Bosch 1996; Harris & Wanless 1997; Bosch *et al.* 2000; Blackwell *et al.* 2000a; Guillemette & Brosseau 2001; Martinez-Abrain *et al.* 2004; Wanless *et al.* 2006). However, these strategies can have unforeseen effects.

Making gull eggs unviable through the use of techniques like oiling has long been identified as a means to control problem populations (Patten & Patten 1977; White *et*

al. 1979; Blokpoel & Hamilton 1989). However, to ensure effectiveness it is important to get the timing of application correct. Applying oil to an egg late in the incubation period greatly reduces its efficacy (Lewis & Malecki 1984). However, to minimise the number of clutches abandoned, and therefore re-nesting attempts, application later in the nesting period is recommended (Blackwell *et al.* 2000a). Even when properly applied, techniques to reduce the viability of eggs can have mixed results. The effects of recruitment from elsewhere can negate any positive effects this strategy has (Wanless *et al.* 1996). Furthermore, making eggs unviable can actually increase colony reproductive success (Martinez-Abrain *et al.* 2004). By reducing the number of successfully hatched chicks, the territory available to those which do hatch is increased, thereby reducing the effects of intra-specific competition.

A number of attempts have been made to control problem gull populations using culls (Coulson *et al.* 1982; Bosch 1996; Harris & Wanless 1997; Bosch *et al.* 2000; Guillemette & Brousseau 2001). Often this is done to improve the survival and breeding success of threatened species. This can have mixed results on the species concerned, even when they live in the same geographic area. On the Isle of May gulls were culled between 1972 and 1988 (Harris & Wanless 1997; Finney *et al.* 2003), whilst the reduction in density improved the recruitment of the Atlantic puffin (*Fratercula arctica*) it had no effect on the recruitment of the oystercatcher (*Haematopus ostralegus*). As a result of ecological characteristics, like density dependence, dispersal and meta-population dynamics (Coulson *et al.* 1982; Wanless *et al.* 1996; Bosch *et al.* 2000), many of these culls also had a limited effect on the gull populations concerned.

The key to developing an effective control strategy is to consider the ecology of the system concerned. It is not only necessary to know where a species is, but also when it is there and how this influences the problem under consideration. This requires a thorough examination of spatial and temporal trends in not just the distribution of the species involved, but also the problem concerned. However, these trends are often subject to a series of complex, interacting relationships. Disentangling these effects can often be difficult, if not impossible when using traditional techniques, therefore, more advanced analytical methodologies are needed.

By investigating factors determining the distribution of gulls throughout the year, it is possible to suggest effective control strategies for problem colonies, like those inhabiting town centres. Control strategies are more likely to be effective during the summer when distributions are constrained by breeding attempts and can be more easily predicted. This thesis has identified features, for example easy access to local food supplies, that can attract gulls to specific areas. By reducing this access, in combination with efforts to reduce breeding success, breeding colonies are likely to disperse elsewhere. However, it is important to take the surrounding area into account to avoid simply moving the problem to the next town along. These efforts could be greatly improved by a better understanding of how gulls disperse between summer breeding sites and winter roost sites.

In the past, the use of statistics in ecology was viewed as "a sign of decadence, rather than progress" (Ashby 1936). This opinion is still held by some researchers today, with some feeling that statistics are "just another technique" (*Personal observation*).

However, because ecological datasets are often more complex than they first appear, statistics are an integral part of research.

Ecological datasets often include the repeated measurement of a number of individuals or sites over a given time period. Additionally, measured variables often display natural variation across their geographic range. This can lead to problems such as pseudo-replication and spatial or temporal autocorrelation. These issues have received growing attention in recent years as they lead to violations of assumptions of identically and independently distributed errors (i.d.d.). Violating these assumptions can lead to an inaccurate estimation of both the coefficients and the significance of a model (Hurlbert 1984; Legendre 1993; Koenig 1999; Lichstein *et al.* 2002; Segurado *et al.* 2006; Dormann 2007; Dormann *et al.* 2007). A suite of statistical approaches have been advocated in order to counter these problems including, mixed effects models, generalised least squares regression and autocovariate regression (Pinheiro & Bates 2000; Keitt *et al.* 2002; Legendre *et al.* 2002; Segurado & Araujo 2004; Dormann *et al.* 2007; Kissling & Carl 2007).

The flexibility of mixed effects models has meant that they are increasingly being used to model datasets involving repeated measures (i.e. Buckley *et al.* 2003; Scherber *et al.* 2006; Balbontin *et al.* 2007; Cook *et al.* 2008). They enable us to model correlations existing within data grouped by individual experimental units, for example individuals or sites, by setting these units as random effects (Pinheiro & Bates 2000). By treating a variable as a random effect, deviations in the intercepts (for example, for each individual or site) are treated as random deviations from a mean

population value. This has the further advantage that it uses up fewer degrees of freedom than treating variables as fixed effects with multiple levels.

Mixed effects models offer the potential to account for spatial autocorrelation within repeated measures datasets with the inclusion of a variance-covariance matrix (Pinheiro & Bates 2000). When repeated measures are not an issue within the data, there are a variety of strategies that can be adopted. The simplest of these is probably autocovariate regression. Here, an additional covariate based on the distance weighted values of response variables from surrounding sites (Keitt *et al.* 2002; Dormann *et al.* 2007; Aarts *et al.* 2008). This estimates how much the response variable of any given site is influenced by the response variables at surrounding sites and can be included in a generalised linear model (GLM). Such a covariate can be easily computed using the spdep extension (Bivand 2007) of the R statistical package (R core development team 2007). An alternative approach involving GLMs is to fit a negative binomial error structure (i.e. Hartley 1998). The negative binomial distribution is defined as a logarithmic distribution with zeroes compounded with a Poisson distribution (Quenouille 1949). In practice this can be described as an initial invasion of organisms into the study, each of which has a probability of disappearing, whilst those that remain are able to reproduce. As a result, the negative binomial distribution is able to account for ecological processes such as migration, reproduction or mortality which can be influenced by the environment (Binns 1986). A key feature of this distribution is that it relaxes assumptions of independence made by the Poisson, and other distributions (White & Bennetts 1996). By using negative binomial GLMs it was possible to more accurately explain the distribution of gull roosts. Low values of θ indicated strong aggregation amongst these roosts for all species, and a failure to

account for this would have led to a inaccurate estimates of the coefficients and significance of explanatory variables.

Alternative approaches to GLMs that can be employed to account for autocorrelated data include generalised least squares (GLS) and autoregressive models (i.e. Lichstein *et al.* 2002; Ferrer-Castan & Vetaas 2004; Tognelli & Kelt 2004; Kissling & Carl 2007). As with mixed effects models, GLS directly models spatial autocorrelation using a variance-covariance matrix (Dormann *et al.* 2007). In contrast, autoregressive models use matrices specifying the strength of interactions between sites to model the error generating processes. There are two forms of autoregressive model, the simultaneous autoregressive model (SAR) and the conditional autoregressive model (CAR). The main difference between these is that the CAR model only accounts for first order neighbourhood effects whereas, the SAR model can account for higher order neighbourhood effects (Lichstein *et al.* 2002).

Another common feature of ecological datasets is the presence of correlated and often interacting covariates. To counteract these difficulties, a number of authors have used structural equation models (SEMs) (i.e. Palomares *et al.* 1998; Iriondo *et al.* 2003; Elmhagen & Rushton 2007). When using SEM, a hypothesised model of multiple multivariate relationships is constructed based on an *a priori* knowledge of the system concerned (Grace 2006). This can then be challenged with the data until a simplified, parsimonious model remains. Landfill use by gulls is often subject to a series of interacting, and often correlated effects. Consequently, previous studies have tended to focus on a limited range of variables (i.e. Coulson *et al.* 1987; Belant *et al.* 1993; Karlsson 2003; Bellebaum 2005). By using SEM it was possible to disentangle the

complex relationships surrounding landscape use by gulls and to highlight seasonal variation as an important, driving factor.

All of these methodologies are readily implementable in the statistical package R and its extensions. Increasing computer power has frequently revolutionised the way in which scientists view and use statistics (Boyce 2002), making it easier to disentangle the often complex interactions occurring between organisms and the environment they use. However, there remains a concern that ecologists are using overly complex statistical techniques with the aim of publishing research in higher profile journals, rather than to gain additional biological insights from their data (Murtaugh 2007)

Whilst statistics are integral to ecological research, their correct use and interpretation are equally important. Ecological journals frequently publish in excess of 2 400 p-values on an annual basis, almost half of which have no further information on either means or effects sizes (Cherry 1998; Anderson *et al.* 2000). Consequently, the correct application, interpretation and use of statistics in ecology has been the source of much debate recently (Anderson *et al.* 1994; Johnson 1999; Anderson *et al.* 2001; Burnham & Anderson 2002; Stephens *et al.* 2005; Whittingham *et al.* 2006; Lukacs *et al.* 2007; Richards 2008).

Many studies have argued recently that researchers are over reliant on p-values when reporting their results (Cherry 1998; Johnson 1999; Anderson *et al.* 2000; Fidler *et al.* 2004; Lukacs *et al.* 2007; Nakagawa & Cuthill 2007), with greater emphasis placed on statistical rather than biological significance. The arbitrary nature of the p-value leads researchers to "abdicate their responsibility to evaluate the significance of a

result to a caned, cookbook procedure" (Cherry 1998). Consequently, there is a growing pressure to report effect sizes and their confidence intervals alongside, or instead of the p-value (Johnson 1999; Osenberg *et al.* 2002; Nakagawa & Cuthill 2007). This provides an illustration of both the magnitude and direction of any effect, rather than merely whether an effect is present or not. Where the standard errors lead to the effect sizes overlapping with zero, it can be said that there is no significant effect.

These developments have gone hand in hand with the increasing support for information theoretic (IT) approaches when interpreting ecological data, at the expense of traditional null hypothesis testing (Burnham & Anderson 2002; Johnson & Omland 2004; Rushton *et al.* 2004; Stephens *et al.* 2005; Stephens *et al.* 2007; Lukacs *et al.* 2007). Traditional null hypothesis testing uses parameter inference (i.e. determining whether or not variables are statistically significant) to determine whether or not variables warrant inclusion in a final model. This has led to concerns over biases in parameter estimates, over-fitting and incorrect significance tests (Whittingham *et al.* 2006). The starting point for the IT approach is to formulate a series of models based on an understanding of the system concerned. These are then compared using Aikaike's information criterion (AIC) to determine which model is closest to reality, whilst at the same time penalising for the number of variables included in the model (Rushton *et al.* 2004). The advantage of an IT approach is that rather than relying on arbitrary measures of significance to decide whether a variable warrants inclusion in a final, parsimonious model, it can use a value, like the AIC, which can be compared between models using likelihood ratio tests (Burnham & Anderson 2002). Consequently, the IT approach often provides a final model with a

better fit and therefore greater understanding of the system (Greaves *et al.* 2006; Whittingham *et al.* 2006)

In order to make valid statistical inference, it is vital that an appropriate model is selected (Stanley & Burnham 1999). The "true" model for any data is unlikely to be known, it is therefore important to select one which is plausible and balances model bias and sampling variance. However, by increasing the pool of covariates included in a model, the ability of any model selection approach to distinguish between those which are informative and those which are non-informative is greatly diminished (Murtaugh 1998). Those models which contain factors which are not significantly different from zero provide a poor basis for statistical inference (Anderson *et al.* 1994).

However, the correct interpretation of statistics is a moot point if the data (including both response and explanatory variables) have not been collected in an organised and systematic fashion. The use of statistics is not, and should not be regarded as a substitute for this. The collection of ecological data can be an expensive and labour intensive process. Anderson (2001) highlights two major concerns about the collection of field data, the use of "convenience" sampling, collecting data from points readily accessible to the researcher, such as those close to roads or paths, and the use of index values purporting to measure relative abundance. The major criticism of convenience sampling is its reliance on anthropogenic landscape features, like roads or paths, which are unlikely to be representative of the system as a whole. Despite this, convenience sampling is still widely used in ecology (Rosenstock *et al.* 2002).

The problems posed by the use of index values, for example the use of raw count data to estimate relative abundance, can be well illustrated by the debate about the utility of top predators for monitoring biodiversity (Sergio *et al.* 2006; Roth & Weber 2008; Kery *et al.* 2008; Sergio *et al.* 2008). Sergio *et al.* (2006) found that top predator abundance in any given area could be correlated with its biodiversity. Much of the subsequent criticism of this hypothesis focussed on the apparently low number of species recorded in the study area, compared to previous estimates for comparable neighbouring areas (Kery *et al.* 2008). In response, Sergio *et al.* (2008) highlighted a number of differences in survey technique including differences in observer effort, skill and species detectability. This shows that estimates can often vary depending on the methodology used. To counteract this problem, Pollock *et al.* (2002) advocate the inclusion of an estimate of detection probability when estimating factors such as species abundance.

In any study it is easy to envisage a huge number of covariates that could potentially be affecting the response. However, concern has been raised in the literature about practices such as exploratory data analysis and "data-dredging" (Olden & Jackson 2000; Anderson *et al.* 2001; Lukacs *et al.* 2007), whereby researchers have been unclear about their ultimate objectives and have consequently measured everything that is measurable. These circumstances present problems for two reasons. Firstly, by including a large number of variables, measures of fit, like R^2, are likely to be high, even when relationships may be weak or non-existent (Freedman 1983). By refitting such a model, with variables which have a low t value excluded, the overall F value may become highly significant, leading to spurious estimates of significance.

Secondly, by increasing the size of the covariate pool, the ability of model selection techniques to discriminate between informative and non-informative variables is decreased (Murtaugh 1998). Consequently, it is important to set clear hypotheses and objectives, based on *a priori* knowledge of the system concerned, before conducting any analysis.

The results of such analysis can be used to inform decision making for management strategies. However, despite the rapidly growing vertebrate pest control industry (BPCA 2006), with the annual cost of control at one site estimated at between US$65-120,000 per annum (Allan 2002) there is no clear consensus on effective strategies or techniques. Whilst around 527 studies have been carried out on techniques to control problem gull populations (Google Scholar search terms; pest, gull, control in biology, life sciences and environmental science, accessed 17/10/2008) a large proportion of these have been reported only in conference proceedings and other "grey" literature. Furthermore, few studies (i.e. Baxter & Robinson 2007; Cook *et al.* 2008; Soldatini *et al.* 2008) have attempted to compare the efficacy of a range of techniques, instead focussing on whether or not a single technique, such as the use of raptors, poison, distress calls or shooting, is effective or not (i.e. Bomford & O'Brien 1990; Seamans & Belant 1999; Blackwell *et al.* 2000b: Seamans *et al.* 2002; Baxter & Allan 2006; Baxter & Allan 2008). By comparing a range of techniques in this thesis, it was possible to comment on their relative efficacy and to identify common features which can be further developed in subsequent studies. Overall, those techniques in which the birds could perceive a "genuine" threat, for example the use of birds of prey, were less prone to habituation and had a greater initial influence than those which sought merely to harass pests.

As previously outlined, one possible explanation for the lack of published, peer reviewed studies on control strategies is the difficulty some researchers have in disentangling the often complex, interacting processes involved in pest ecology. However, there are two additional explanations for the lack of this information, which may prove just as important. Several authors have identified publication bias as a problem in ecology (Csada & James 1996; Jennions & Moller 2002) whereby non-significant results are less likely to be published. This is of particular concern in applied ecological problems, like pest control, where it can be just as important to know what techniques are ineffective as which ones are effective.

Control of animals regarded as pest species can prove deeply unpopular in the court of public opinion, with a number of organisations actively campaigning against it (i.e. PETA 2008; AnimalAid 2008). Consequently, scientists involved in research into control strategies often find it difficult to publish their findings because private companies, which fund such research, are reluctant to be seen to be involved (J. Allan *personal communication*). However, evidence from recent research suggests that ensuring the public are kept informed about, and understand the need for, any control strategies, such controversy can be averted (Barr *et al.* 2002; Bremner & Park 2007). There is an urgent need for greater discussion of population management and control, both effective and ineffective, in the scientific press.

Many investigations into human-wildlife conflict, for example zoonotic disease or bird strike risk, seek merely to identify whether or not a problem exists (i.e. Richards & West 2000; Thorpe 2003; Boqvist & Vagsholm 2005; Dekker *et al.* 2006; Hughes

et al. 2008; Philbey *et al.* 2008). Attempts are then made to mitigate the problem without further investigation into the underlying ecology. However, as the species concerned are not uniformly distributed in space and time, the problems they cause are not likely to be either. Consequently, this approach is unlikely to be either efficient or effective. Therefore, having identified the problem, it is then necessary to quantify spatial and temporal variations in its occurrence.

Efficient and effective management strategies require that the distribution patterns of any problem are then combined with the distribution patterns of the species concerned. The life history of gull species means that they have different ecological requirements in the summer and winter. During the summer, their habitat use is restricted by the requirements associated with provisioning for young (Pierotti & Annett 1991), whilst in the winter the UK population is swollen by an influx of migrants from Scandinavia and continental Europe (Wernham *et al.* 2002). An effective control strategy must identify and take this variation into account.

Having identified the patterns of variation in both the underlying problem and the distribution of the species causing the problem, it is possible to consider potential solutions. The appropriate solution must take into consideration the nature and scale of the problem and what aspect of the species ecology causes the problem. It will vary according to situation concerned.

It is impractical to reduce collisions between aircraft and gulls by attempting to influence the distribution and movements of gulls. As a result, ornithologists, civil and military aviation agencies work together to develop bird avoidance models

(BAMs) (i.e. Lovell & Dolbeer 1999; Zakrajsek *et al.* 2000; van Belle *et al.* 2007). However, many BAMs operate at too coarse a scale to be of practical use. This thesis has demonstrated that strikes by gulls on RAF aircraft are clustered around both landfill sites and large (>1000 individuals) gull roosts (which pose a particularly high risk to military aircraft). Furthermore, a large proportion of those strikes which have involved species of unknown identity are also likely to have involved gulls. By understanding what landscape features influence the distribution as well as the spatial scale this influence acts over and how it varies with altitude, it is possible to begin the development of a more effective and realistic Bird Avoidance Model. There is plenty of scope for the improvement of this model with the inclusion of additional data, such as weather and the seasonal patterns in avian behaviour, however, this is the first time that a spatial relationship has been demonstrated between gull strikes and roosts.

When attempting to keep gulls away from areas like landfill sites or airports, one of the multitude of deterrence techniques available may be effective. However, many of these are prone to habituation (Gilsdorf *et al.* 2002; Soldatini *et al.* 2008). Techniques like falconry appear less susceptible to habituation (Cook *et al.* 2008). This may be because they appeal to gulls natural predator avoidance instinct, or alternatively a response to the stimulus of observing the death of conspecifics. Even the more effective deterrence techniques should not be used in isolation from other strategies. Habitat management through the reduction of standing water and an increase in grass length has been shown to be effective at reducing the number of bird strikes on and around airfields (Brough & Bridgman 1980; Buckley & McCarthy 1994; Gabrey & Dolbeer 1996). Around sewage outflows and landfill sites, altering the supply of the resource attracting the gulls to the area in the first place can prove effective at

preventing numbers becoming problematic (Ferns & Mudge 2000; Raven & Coulson 2001; Burger 2001). These strategies in combination with deterrence techniques can act to deter populations from gathering in areas where they present a problem and then make the areas less attractive to the species.

Whilst this may prove effective at dispersing gulls from feeding or loafing areas, it is only effective at dispersing gulls from roost sites where there are alternative sites nearby (Gosler *et al.* 1995). Consequently, it is important to understand what features are attracting gulls to roost in the area, and also what is hoped to be achieved as a result of clearing gulls from the site. To limit the damage caused by a gull roost it is likely that strategies, like culling and egg oiling, will be required in order to keep the population size under control.

With the range of strategies available to control populations, it is important to select one that is appropriate for the situation in hand. Ultimately however, any strategy must attempt to take into account the ecological reasons for whatever problem it sets out to solve.

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